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RECORDS OF THE BRYOZOAN FAMILY SELENARIIDAE FROM WESTERN AUSTRALIA AND SOUTH AUSTRALIA, WITH THE DESCRIPTION OF A NEW SPECIES OF SELENARIA BUSK, 1854

S. A. PARKER & P. L. COOK

Summary

Unlike that of Bass Strait, the selenariid of southern Western Australia and South Australia is relatively poorly known. A first estimate of its diversity is presented here, based on a study of 514 colonies (in 100 samples), mostly previously unreported species collected by Sir Joseph Verco (1851 – 1935). The study confirms an earlier suspicion that *Selenaria hexagonalis* Maplestone, 1904 actually consists of two species, here distinguished as *S. hexagonalis sensu stricto* and *S. verconis* sp. nov. In all, 16 species are represented, of which 11 now constitute new records for the region (South Australia: *Otionella nitida* (Maplestone, 1909) *O. australis* Cook & Chimonides, 1985b, *Selenaria punctata* Tenison-Woods, 1880, *S. concinna* Tenison-Woods, 1880, *S. varians* Cook & Chimonides, 1987, *S. exasperus* Cook & Chimonides, 1987, *S. verconis* sp. nov. and ‘*S.* *alata* auctt. (non Tenison-Woods, 1880); Western Australia: *S. bimorphocella* Maplestone, 1904, *S. concinna*, *S. hexagonalis* and *S. verconis* sp. nov). Brief description of the genera and species are provided.

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S. A. PARKER & P. L. COOK

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Unlike that of Bass Strait, the selenariid fauna of southern Western Australia and South Australia is relatively poorly known. A first estimate of its diversity is presented here, based on a study of 514 colonies (in 100 samples), mostly previously unreported specimens collected by Sir Joseph Verco (1851–1935). The study confirms an earlier suspicion that *Selenaria hexagonalis* Maplestone, 1904 actually consists of two species, here distinguished as *S. hexagonalis sensu stricto* and *S. verconis* sp. nov. In all, 16 species are represented, of which 11 constitute new records for the region (South Australia: *Otionella nitida* (Maplestone, 1909), *O. australis* Cook & Chimonides, 1985b, *Selenaria punctata* Tenison-Woods, 1880, *S. concinna* Tenison-Woods, 1880, *S. varians* Cook & Chimonides, 1987, *S. exasperans* Cook & Chimonides, 1987, *S. verconis* sp. nov. and '*S.* *alata* auctt. (non Tenison-Woods, 1880); Western Australia: *S. bimorphocella* Maplestone, 1904, *S. concinna*, *S. hexagonalis* and *S. verconis* sp. nov). Brief descriptions of the genera and species are provided.

S. A. Parker¹, South Australian Museum, North Terrace, Adelaide, South Australia 5000, and P. L. Cook, Associate, Museum of Victoria, Swanston Street, Melbourne, Victoria 3000. Manuscript received 22 March 1993.

The calcareous element of southern Australian shelf sediments contains in places a high proportion of living bryozoans and dead bryozoan skeletons (Wass *et al.* 1970, James *et al.* 1992). Although many bryozoans live in or on such sediments, the free-living cup-shaped (lunulitiform) species of the anascan family Selenariidae can be particularly abundant in this zone. However, no idea of the abundance and diversity of selenariids in southern Australia was received until the appearance of Cook and Chimonides's studies on the Australasian Selenariidae (Cook & Chimonides 1984a, b, 1985a–c, 1986, 1987). From the Tertiary to the Recent of southern Australia (mainly Victoria and Bass Strait), these authors listed four genera (one new) and 43 species (18 new), many of the latter with an extensive temporal, and sometimes a wide geographical, range.

The marine invertebrate collections of the South Australian Museum include much material obtained by Dr Sir Joseph Verco in the years 1890–1912. Verco was principally interested in molluscs, and the chief method he employed to obtain these (dredging) resulted in the collection of other benthic groups such as brachiopods (Verco & Blochmann

1910), turbinoliid scleractinians (Cairns & Parker 1992) and selenariid bryozoans.

In 1904, in correspondence to Sir Sidney Harmer, C. M. Maplestone mentioned Verco's selenariid collections, and offered to have specimens of his own new species *Selenaria hexagonalis* and *S. bimorphocella*, sent to Harmer by Verco. Subsequently, Livingstone (1928), in discussing Verco's bryozoans in the SAM, listed two samples under *Selenaria punctata* Tenison-Woods and one under *Lunularia capulus* (Busk); comments on these identifications are given below.

Apart from these instances, Verco's selenariids have remained unreported. Inasmuch as his collecting stations ranged from the south-east of South Australia (off Beachport and Cape Jaffa) westward to the Albany and King George Sound districts of Western Australia, they complement those reported by Cook and Chimonides, which were mainly in the Bass Strait, with one off Jurien Bay near Perth.

Verco's selenariid material in the SAM numbers 48 samples. This was augmented by other material, including 19 Verco samples in the QM, four samples from off Perth, 1963 (QM), four from Western Australia (WAM) and four from South Australia, 1982–1991 (SAM). The following article lists the 16 species involved, together with synonymies, references to recent redescriptions, details of material examined, notes on Recent and

¹ (Shane Parker died in November 1992. This paper was then in the final stages of preparation, P.L.C.).

fossil distribution and bathymetric range, and remarks on the distinguishing features of the species and genera.

MATERIALS AND METHODS

Abbreviations of institutions referred to in this paper are: BMNH, Natural History Museum, London; NMV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth.

Five hundred and fourteen specimens (colonies) in 100 samples were examined, of which 406 specimens in 69 samples were collected by Sir Joseph Verco. By institution, the material was constituted as follows: SAM: Verco Coll. 268(48), other sources 78(20); QM: Verco Coll. 136(19), other sources 5(4); NMV: Verco Coll. 1(1), other sources 1(1); BMNH: Verco Coll. 1(1), other sources 2(2); WAM: other sources 22(4). Among the specimens examined were five syntypes of *Lunulites patelliformis* Maplestone, 1904 (= *Lunularia capulus* Busk, 1852a) and the lectotype of *Selenaria hexagonalis* Maplestone, 1904. All specimens were Recent except for a Pliocene paratype of *S. verconis*. Unless otherwise specified, all specimens referred to under *Material Examined* were collected by Verco.

NOTES ON LUNULITIFORM COLONIES

Although some lunulitiform colonies are attached by rhizoids to shell fragments etc., on the sea-bottom, the free living species are unattached and are stabilized and supported by the elongated avicularian mandibles of the peripheral regions of the colony. Some species are capable of locomotion (see Cook & Chimonides, 1978 and Chimonides & Cook, 1981). They live in, or upon the upper centimetres of sediment, where their dead skeletons also accumulate. Colonies rarely exceed 25 mm in diameter and are conical, cup-shaped or discoid. Each colony, whether spirally or radially budded, has patterned groups of feeding zooids (autozooids) and avicularia, which have elongated, paddle-shaped or whip-like mandibles. Large brooding zooids tend to be found subperipherally or peripherally, and in the genus *Selenaria*, very large, specialized, non-feeding male zooids occur peripherally among enlarged avicularia.

Some species, or populations within species, seem to have particular depth and/or temperature tolerances. For example, living *Selenaria maculata* is common in only 2–4 m in Queensland, but has been found at 146 m in New South Wales; *Otionella*

affinis thrives at nearly 250 m off New Zealand. Generally, the most abundant and diverse living fauna seems to occur between 50 and 130 m depth. The material examined here shows few exceptions, but nearly all the best preserved colonies with mandible and frontal membranes intact, which may be inferred to have been alive when collected, occur from depths shallower than 60 m. The exceptions are *Helixotionella spiralis* and *H. scutata*, which together with *S. pulchella* were all originally collected alive from off Jurien Bay, Western Australia at 137 m. All three species were collected alive by Verco from off Albany at 147 m (see below), which suggests that their tolerances are normally at the deeper end of the range.

SYSTEMATICS

Order Cheilostomatida Busk, 1852b

Suborder Anasca Levinsen, 1909

Superfamily MICROPOROIDEA Gray, 1848

Family SELENARIIDAE Busk, 1854

Genus *Lunularia* Busk, 1884

Zooids large with limited cryptocyst, budded radially; avicularia large, simple, with paddle-shaped mandibles; large brooding zooids scattered.

Lunularia capulus (Busk, 1852a)

Lunulites capulus Busk, 1852a: pl. 1, figs 13, 14. 1854: 100, pl. 112.

Lunulites gibbosa Busk, 1854: 100, pl. 111.

Lunulites patelliformis Maplestone, 1904: 215, pl. 25, fig. 6.

Selenaria livingstonei Bretnall, 1922: 190, figs 2, 2a.

Lunularia capulus: Livingstone 1924: 198, 1928: 115; Cook & Chimonides, 1986: 691, figs 6, 9, 12–14.

Material Examined

South Australia: Petrel Bay, St Francis I., 19 fms (34.8 m), SAM L532(1); 13 Nm (nautical miles) (23.8 km) ESE of Troubridge Point, 35 m, K. L. Gowlett-Holmes and S. Corigliano 11–12.vi.1991, SAM L675(1); Investigator Strait, 20 fms (36.6 m), SAM L395(1); Gulf St Vincent, SAM L492–496(5) (syntypes of *Lunulites patelliformis* Maplestone); W of Aldinga, Gulf St Vincent, 38–41 m, K. L. Gowlett-Holmes and S. Corigliano 4–5.v.1987, SAM L533(1); Emu Bay, Kangaroo I., ca 35 m, J. Gehling 4.iv.1984, sandy bottom, SAM L549(2); no data, SAM L535, 536(2).

Distribution

Previously known from Torres Straits, Queensland, New South Wales, Victoria, Bass Strait (including Bank Strait between Flinders I. and Tasmania), South Australia and south-western Western Australia, 27.5–167 m, with fossil records from the Miocene and Pliocene of Victoria and the Pliocene of South Australia and Western Australia. Previous South Australian records are from Investigator Strait, Gulf St Vincent and Backstairs Passage; the present material adds St Francis I. and Kangaroo I. to the known range in that State.

Remarks

Of the 13 colonies examined, seven were alive when collected. *L. capulus* is characterized by its large, deeply domed zoaria, and autozooids and avicularia alternating in distally contiguous radial series. The three colonies of L549(2) and L675(1) are the largest so far seen by us, measuring 34, 34 and 35 mm in diameter respectively.

One of the two colonies of L549 bears on its basal surface good examples of basal buds (structures previously described by Cook & Chimonides, 1986: 697–698).

The sheltered, strongly concave basal surface of *L. capulus* is often colonized by other bryozoans. In the present specimens, the most frequent of these is the microporid *Mollia multijuncta* (Waters, 1879), which occurs in samples L492, L532, L549 and L675. The two zoaria of L549 bear also basal colonies of a species of *Arachnopusia* Jullien, 1888, *Chorizopora brongniartii* (Audouin, 1826), *Microporella lunifera* Haswell, 1880 and three species of *Parasmittina* Osburn, 1952. Apart from the small area of *M. multijuncta*, L675 is almost completely encrusted basally with *Membranipora perfragilis* (MacGillivray, 1881), and supports also a small colony of *Scrupocellaria* sp. and a minute individual (3 mm diameter) of a scleractinian coral, probably *Scolymia australis* (Milne Edwards & Haime, 1849). On the basal surface of L533 occurs yet another bryozoan, *Crassimarginatella pyrula* (Hintcks, 1881).

Cook (1985: 23–24, 93) discussed the occurrence of acrothoracid cirripedes in large lunulitiform bryozoans, particularly that of *Kochlorinopsis discoporellae* Stubbings, 1967 in West African populations of the cupuladriid bryozoan *Discoporella umbellata* (Defrance, 1823). In our material, these barnacles have been present in samples L492, L532, L533 and L675, as attested by the small slits at the apex of the colonies.

Lunularia repanda (Maplestone, 1904)

Lunulites repandus Maplestone, 1904: 216, pl. 25, fig. 7.

Lunularia repandus: Cook & Chimonides, 1986: 698, figs 7, 8, 10, 15, 16.

Material Examined

Western Australia: 32°S., 115°08'E., off Perth, 119 m, B. Jamieson 28.viii. 1963, QM GH1150(1); King George Sound, 12–14 fms (22–25.6 m), SAM L537(1), 28 fms (51 m), SAM L538(1), 35 fms (64 m), QM GH1693(1); 80 Nm (146.4 km) W of Eucla, 81 fms (148 m), iii.1912, SAM L539(1), 140 fms (256 m), SAM L540(1).

South Australia: Off St Francis I., 35 fms (64 m), SAM L541(1); cove NW of Petrel Cove, St Francis I., 40 m shifting sandy bottom, W. Zeidler & N. Holmes 28.i.1982, SAM L548(3); S of Troubridge I., 20 fms (36.6 m), SAM L542(1); Beachport, 150 fms (275 m), SAM L543(1); no data, SAM L534(1), L544–547(36).

Distribution

Previously known from south-western Western Australia, South Australia and Bass Strait (27.5–183 m) and from the Kermadec Ridge (145–350 m; see Gordon, 1984), and by fossils from the Miocene of New Zealand. The present material adds King George Sound and 80 Nm (146.4 km) W of Eucla to the known Western Australian range, and St Francis I. and Beachport to the known South Australian range, and increases the recorded depth-range to 22–275 m.

Remarks

Of the 49 colonies examined, 29 were alive when collected. *L. repanda* differs from *L. capulus* in having flatter zoaria, and the autozooids in radial series not alternating with series of the avicularia which are very large and scattered. One sample (SAM L547) comprised 18 colonies, several of which exceeded 29 mm in diameter. Colonies in SAM L542 and L548 bore the bryozoan *Mollia multijuncta* (Waters, 1879) (Microporidae) on their basal surfaces.

Genus *Otionella* Canu & Bassler, 1917

Zooids budded radially, with small, rounded opesia. Ancestrula with one distal and one proximal adjacent avicularium. Brooding zooids enlarged, marginal.

Otionella squamosa (Tenison-Woods, 1880)

Selenaria squamosa Tenison-Woods, 1880: 29, fig. 29.

Otionella squamosa: Cook & Chimonides, 1984a: 232, figs 2, 6, 7, 14 g,h, 15, 21E; 1985b: 586, figs 16, 17; Gordon, 1986: 71, pl. 28C.

Material Examined

?South Australia: no data, SAM L550(1).

Distribution

O. squamosa has been reported from Torres Strait, New South Wales, Bass Strait (20–121 m) and New Zealand (1092.5 m), and as a fossil from Victoria and Bass Strait (Pliocene) and New Zealand (Pleistocene). The present specimen, though without details of provenance, is most likely from South Australia.

Remarks

O. squamosa is distinguished by its large, scattered, usually asymmetrical avicularia, with marginally perforated cryptocyst, and prominent condyles unfused or fused on the basal side only.

Otionella nitida (Maplestone, 1909)

Selenaria nitida Maplestone, 1909: 271, pl. 77, fig. 8.

Otionella nitida: Cook & Chimonides, 1984a: 239, figs 14f, 16, 18–20, 21B; 1985b: 584, figs 14, 15, 29.

Material Examined

South Australia: Backstairs Passage, 'deep water', SAM L551(1); Cape Jaffa, QM GH1642(1); no data, SAM L552(4), L553(1).

Distribution

Previously known from south-western and mid-western Western Australia, Bass Strait and New South Wales (17–148 m), with fossil records from south-western Western Australia (Pliocene) and New Zealand (Pleistocene, Miocene). The present material adds South Australia to the Recent distribution of the species.

Remarks

Of the seven colonies examined, two were alive when collected. Colonies of *O. nitida* are very small and domed; the small, symmetrical avicularia, which may occur in contiguous radial series, have a perforated cryptocyst and fused condyles.

Otionella australis Cook & Chimonides, 1985b

Otionella australis Cook & Chimonides, 1985b: 590, figs 11, 12, 23–25.

Material Examined

Western Australia: 32°S., 115°08'E., off Perth, 119m, B. Jamieson 28.viii. 1963, QM GH1150(2); King George Sound, 35 fms (64 m), QM GH1693(3); 80 Nm (146.4 km) W of Eucla, 81 fms (148 m), iii.1912, SAM L554(49); W of Eucla, 50–

120 fms (92–220 m), iii.1912, SAM L555(4); 40 Nm (73.2 km) W of Eucla, 72 fms (132 m), iii.1912, SAM L556(2).

South Australia: Cape Jaffa, QM GH1642(55); off Cape Jaffa, 90 fms (165 m), SAM L557(1), 130 fms (238 m), SAM L558(1); no data, SAM L559(1), L560(2).

Distribution

Previously known from south-western Western Australia and Bass Strait, 84–137 m and in the fossil record from south-western Western Australia (Pliocene) and Victoria (Miocene). The present material adds South Australia (south-eastern) and the Western Australian sector of the Great Australian Bight to the species' known distribution, and extends the depth-range to 238 m.

Remarks

Of the 62 colonies in the SAM, 25 were alive when collected. *O. australis* is distinguished by the simple, scattered, almost symmetrical avicularia with long serrated opesia and large unfused condyles. Most specimens examined (dried or in alcohol) were of a pale blue or deep reddish colour.

Genus *Helixotionella* Cook & Chimonides, 1984b

Zooids budded in paired interdigitating spirals. Avicularia with setiform mandibles. Brooding zooids with enlarged opesia.

Helixotionella spiralis (Chapman, 1913)

Selenaria marginata var. *spiralis* Chapman, 1913: 184, pl. 18, fig. 33.

Helixotionella spiralis: Cook & Chimonides, 1984b: 257, figs 6–10, 13, 14, 17, 18, 1987: 962.

Material Examined

Western Australia: 32°S., 115°08'E., off Perth, 119 m, B. Jamieson 28.viii. 1963, QM GH1150(1); 80 Nm (146.4 km) W of Eucla, 81 fms (148 m), iii.1912, SAM L561(2).

Distribution

Previously known from 40 km west of Jurien Bay, Western Australia, 137.2 m, with fossils from Victoria (Oligocene to Pliocene). The present material adds two localities to the species' range in southern Western Australia (one in the Great Australian Bight), and increases the recorded depth-range to 119–148 m.

Remarks

The two colonies in the SAM were alive when collected. In this species, the paired interdigitating

spirals of zooids form the entire minute colony, which rarely exceeds 2 mm in diameter. The avicularian opesia is serrated and the condyles unfused. There is usually only one pair of basal avicularia.

H. spiralis is remarkable for the extent of its temporal range, from Oligocene to Recent (Cook & Chimonides, 1987: 962).

***Helixotionella scutata* Cook & Chimonides, 1984b**

Helixotionella scutata Cook & Chimonides, 1984b: 265, figs 3–5, 11, 15, 16, 19.

Material Examined

Western Australia: 80 Nm (146.4 km) W of Eucla, 81 fms (148 m), iii.1912, SAM L562(9).

Distribution

Previously known only by the type series from 40 km west of Jurien Bay, south-western Western Australia, 137.2 m. The present material adds the Western Australian sector of the Great Australian Bight to the known distribution of this species, and increases its recorded depth-range to 148 m.

Remarks

The nine colonies examined were all alive when collected. *H. scutata* is distinguished by its bifurcated spiral series of zooids, and by its avicularia having fused condyles and an opesia obscured by a flattened scuta.

Genus *Selenaria* Busk, 1854

Zooids budded radially in successive zones. Central zone of closed zooids, surrounded by autozooids and avicularia. Next zone composed of enlarged, female brooding zooids, next zone of peripheral, non-feeding male zooids. Avicularia large, scattered, with S-shaped or reflexed condyle system, mandibles very long, formed from alternating discs of calcified and cuticular tissue.

***Selenaria bimorphocella* Maplestone, 1904**

Selenaria bimorphocella Maplestone, 1904: 213, pl. 24, fig. 3; Cook & Chimonides, 1985a: 301, figs 5d, 15, 16.

Selenaria punctata: Livingstone (non Tenison-Woods) 1928: 114.

Material Examined

Western Australia: 60 Nm (109.8 km) W of Eucla, SAM L563(1); W of Eucla, 50–120 fms (92–220 m), SAM L564 (1); W of Eucla, 72 fms (132 m), QM GH1714(1).

South Australia: 35 Nm (64 km) SW of North Neptunes, 104 fms (190 m), i.1905, SAM L565(3); E of North Neptunes, 45 fms (82 m), SAM L549(1); S of Troubridge I., 20 fms (36.6 m), SAM L567(2); Investigator Strait, 20 fms (36.6 m), SAM L416(3); Investigator Strait, 2 fms (3.7 m), 17 fms (31 m) and 20 fms (36.6 m) QM GH1668(21), and no depth, SAM L568(1); off Point Marsden, Kangaroo I., 15 fms (27.5 m), QM GH1646(4); off Ardrossan, 6–8 fms (11–14.6 m), SAM L373(1); Gulf St Vincent, 12 fms (22 m), QM GH1673(1), 17 fms (31 m), SAM L566(77); Yankalilla Bay, 20 fms (36.6 m), SAM L569(6); Backstairs Passage, 17 fms (31 m), QM GH1636(9) and no depth, SAM L570(56); between Backstairs Passage and The Pages, 25 fms (46 m), SAM L572(1); Cape Jaffa, 90 fms (165 m), QM GH1639(1), 1643(1) Beachport, SAM L572(1); no data, SAM L573–577(32).

Distribution

Previously recorded from South Australia (Gulf St Vincent, Investigator Strait and south of Eyre Peninsula) and Bass Strait, 31–183 m, and as fossils from the Pliocene of Victoria. The present material extends the known range westward to the Western Australian sector of the Great Australian Bight, and adds several localities to the South Australian distribution, notably Cape Jaffa and Beachport in the South-East; it also increases the depth range to 3.7–220 m.

Remarks

Of the 172 SAM colonies examined, 45 were alive when collected; L373 and L416 are the samples reported by Livingstone (1928) as *S. punctata*. A further sample identified by Livingstone (MS) as *S. punctata*, from Yankalilla, consists of five colonies of *S. bimorphocella* (L569) and one of *S. concinna* Tenison-Woods, 1880 (L583).

The colonies of *S. bimorphocella* are large and flat, with very large ancestrulae. The species is distinguished by the considerable sexual dimorphism of the zooids (the male zooids having a trifoliate opesia and no opesiules), and the autozooidal cryptocyst having a sinuate opesia.

Pace Cook & Chimonides, 1985a: 303, *S. bimorphocella* does not replace *S. punctata* along the southern coasts of Australia, for the latter does occur there in small numbers (see below). However, to judge from the large number of samples in the present material, *S. bimorphocella* seems to be by far the commonest selenariid in the region.

***Selenaria punctata* Tenison-Woods, 1880**

Selenaria punctata Tenison-Woods, 1880: 9, pl. 2, figs 8a–c; Cook & Chimonides, 1985a: 303, figs 5e, 9, 10, 17, 19.

Selenaria fenestrata Haswell, 1880: 42.

Selenaria partipunctata Maplestone, 1904: 214, pl. 24, fig. 4.

Material Examined

Western Australia: 32°S., 115°08'E., off Perth, 119 m, B. Jamieson 28.viii. 1963, QM GH1150(1); 80 Nm (146.4 km) W of Eucla, 81 fms (148 m), SAM L578(2); 19°32'S., 118°08'E., NW of Port Hedland, 50–52 m, 26.iii. 1982, WAM 4–92(1); 20°19'S., 116°47'E., off Legendre Id, 42 m, WAM 1864–88(19); Mermaid Sound, Dampier Archipelago, 10.ii.1981, WAM 2–92(1); between Dampier and Port Hedland, WAM 87–89(1).

South Australia: Off Cape Jaffa, 130 fms (238 m), SAM L579(1).

Distribution

Previously recorded from Western Australia, eastern Queensland and New South Wales, 11–137 m, also as a fossil from south-western Western Australia (Pliocene). The present material adds South Australia (South-East) and the Western Australian sector of the Great Australian Bight to the known range of the species, and extends the lower depth-range to 238 m.

Remarks

As noted above, Livingstone's (1928) report of *S. punctata* from South Australia is referred to *S. bimorphocella*. The colonies of *S. punctata* are small, domed, with small ancestrulae; the autozooidal opesiæ are D-shaped with closely-apposed opesiules; brooding zooids have a bar across the orifice, and male zooids have long, paired opesiules. Some of the colonies from Western Australia (SAM) have a diameter of only 3 mm and still retain frontal membranes, but few or no mandibles, many of the others (WAM) are worn. The colony from South Australia is very worn.

The widespread *S. punctata* is very similar to *S. parapunctata* Cook & Chimonides, 1985a, which appears to replace it in Bass Strait (see Discussion). *S. parapunctata* differs by its widely spaced opesiules, absence of an orificial bar in brooding zooids, and S-shaped, rather than reflexed avicularian condyles.

Selenaria pulchella MacGillivray, 1895

Selenaria squamosa var. *pulchella* MacGillivray, 1895: 48, pl. 7, fig. 13.

Selenaria pulchella: Cook & Chimonides, 1984b: 262; 1985a: 307, figs 4, 20.

Material Examined

Western Australia: 80 Nm (146.4 km) W of Eucla, 81 fms (148 m), SAM L580(3).

Distribution

Previously recorded from Jurien Bay, 137 m, south-western Western Australia, with fossils from the Miocene of Victoria. The present sample adds the Western Australian sector of the Great Australian Bight to the species' known range, and increases the depth-range to 148 m.

Remarks

Of the three colonies examined, two were alive when collected. The colonies of this species are minute (2–3 mm in diameter). The zooids have small lateroproximal opesiular indentations, the male zooids possess small paired opesiules, and the avicularia have punctate frontal shields. All three present colonies were sexually mature, with male zooids and large peripheral avicularia, though no mandibles were present.

Selenaria concinna Tenison-Woods, 1880

Selenaria concinna Tenison-Woods, 1880: 10, pl. 2, figs 11a–c; Cook & Chimonides, 1987: 950, figs 1, 11, 24, 28, 30.

Material Examined

Western Australia: 80 Nm (146.4 km) W of Eucla, 81 fms (148 m), SAM L581(1).

South Australia: 35 Nm (64 km) SW of North Neptunes, 104 fms (190 m), i.1905, SAM L582(2); Yankalilla Bay, 20 fms (36.6 m), SAM L583(1); Backstairs Passage, SAM L584(5); Cape Jaffa, 90 fms (165 m), QM GH1643(3).

Distribution

Previously recorded from eastern Queensland, New South Wales, Bass Strait and New Zealand, 33–148 m, and as a fossil from the Pliocene of Western Australia and the Miocene of Victoria. The present material adds South Australia and Western Australia, to the species' known range, and extends the lower depth-limit to 190 m.

Remarks

One of a complex of five very similar species (Cook & Chimonides, 1987), *S. concinna* is distinguished by its avicularia, which have a serrated proximal opesia and a distal calcified bridge. None of the present specimens is larger than 7 mm in diameter, and all are slightly worn.

Selenaria varians Cook & Chimonides, 1987

Selenaria varians Cook & Chimonides, 1987: 957, figs 2, 32, 33.

Material Examined

South Australia: 35 Nm (64 km) SW of North

Neptunes, 104 fms (190 m), i.1905, SAM L585(3); Cape Willoughby, Kangaroo I., 23 fms (42 m), QM GH3160(1).

Distribution

Previously recorded from Bass Strait and New South Wales, 46–95m. The present material adds South Australia to the known distribution of the species, and amplifies the depth-range to 42–190 m.

Remarks

The four colonies examined have a maximum diameter of 4 mm and are all slightly worn. *S. varians* is distinguished by its autozooidal opesiae becoming proportionately larger with astogeny. The avicularia have a marginally serrate opesia.

Selenaria exasperans Cook & Chimonides, 1987

Selenaria exasperans Cook & Chimonides, 1987: 957, figs 5, 12, 34, 35.

Material Examined

South Australia: 35 Nm (64 km) SW of the North Neptunes, 104 fms (190 m), i.1905, SAM L586(2); Cape Jaffa, 130 fms (238 m), SAM L587(1); Cape Jaffa, 90 fms (165 m), QM GH1639(2); Beachport, 110 fms (201 m), SAM L588(2).

Distribution

Previously recorded from Bass Strait and New South Wales, 79–148 m. The present series adds South Australia to the known distribution, and extends the depth-range to 238 m.

Remarks

S. exasperans is distinguished by the presence of a proximo- and disto-lateral avicularium beside the ancestrula, a pattern unique in the genus. Autozooidal opesiae are D-shaped, and avicularian opesiae serrate. All five colonies examined (maximum diameter 4 mm) are slightly worn, but clearly show the ancestrula and adjacent avicularia and autozooids.

Selenaria hexagonalis Maplestone, 1904 (Fig. 1, A)

Selenaria hexagonalis Maplestone, 1904 (part): 214, pl. 24, fig. 5; Cook & Chimonides, 1987 (part): 948, figs 10, 20, 21 (not figs 8, 22, 23, = *S. verconis* sp. nov.)

Material Examined

Western Australia: King George Sound, 28 fms (51 m), SAM L589(1); no data, SAM L590–592(22).

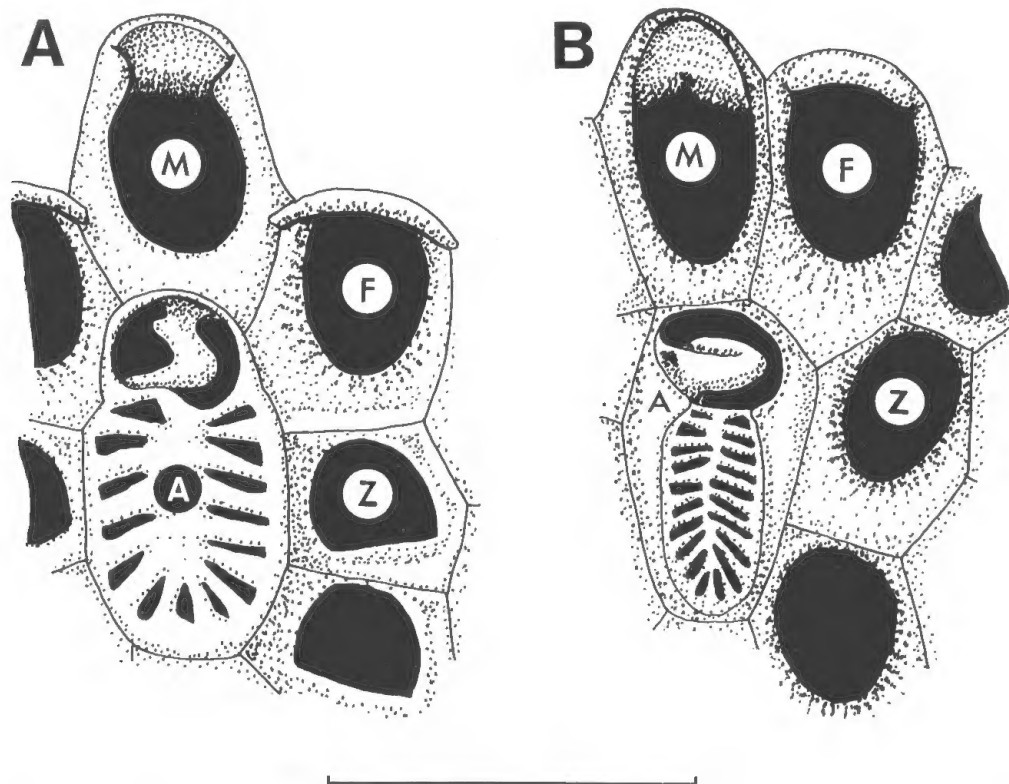


FIGURE 1. Sketches of zooids of *Selenaria*; M, male, F, female, Z, autozooid, A, avicularium. A, *S. hexagonalis* Maplestone. B, *S. verconis* sp. nov. Scale = 0.50 mm.

South Australia: Investigator Strait, 15 fms (27.5 m), NMV P62753, lectotype (selected by Cook & Chimonides, 1987: 948).

Distribution

Known from King George Sound, south-western Western Australia, 51 m and Investigator Strait, South Australia, 27.5 m.

Remarks

Colonies large (diameter 13–15 mm when sexually mature), robust and thickened basally. Autozooids hexagonal in frontal view, with subcentral, almost circular opesia. Centre of operculum just distal to centre of opesia. Subperipheral brooding zooids large, with elongated opesia, raised distally. Peripheral male zooids with very large, oval opesia, without subopercular tubercle. Avicularian shield with 12–16 stout bars, fused medially; condyle system not much reflexed, S-shaped.

The distinctness of this species from the next (*S. verconis* sp. nov.) was suspected by Cook & Chimonides (1987). *S. hexagonalis sensu stricto* has a more restricted range than *S. verconis* sp. nov., being known with certainty from only one district in Western Australia and one in South Australia.

One very large colony (one of the nine in SAM L591), 14 mm in diameter, had apparently ceased growing when 11 mm in diameter, just before sexual maturity. Subsequent growth around the perimeter is marked by swollen basal calcification and concentric series of brooding and male zooids, interspersed with large avicularia. The avicularia are orientated radially, and their condyle systems seem normal, but the frontal shield of bars of calcification is orientated at right angles to the normal direction. The setiform mandibles would not have been affected by the orientation of the frontal shield. The two other mature colonies in this sample show no abnormalities. One of the three colonies in sample SAM L592 has large acrothoracid cirripede burrows in the central area.

***Selenaria verconis* sp. nov.**
(Fig. 1, B)

Selenaria hexagonalis Maplestone, 1904 (part): 214 (Jimmy's Point Farm, Victoria, Pliocene); Cook & Chimonides, 1987 (part): 948, figs 8, 22, 23.

Material Examined

HOLOTYPE: **Queensland:** Off Townsville, 2.5–12 m, coll. Cook & Chimonides, 1982, BMNH 1984. 12.24.14 (illustrated by scanning electron micrographs in Cook & Chimonides, 1987, figs 8, 22, 23).

PARATYPES: **Western Australia:** King George

Sound, 22–28 fms (40–51 m), SAM L593(1), SAM L594(1); ditto, 28 fms (51 m), SAM L594 (1); 40 Nm (73.2 km) W of Eucla, 75–105 fms (137–192 m), iii.1912, SAM L596(1).

South Australia: Off Adelaide, 36–64 m, BMNH 1928.9.13.78.

Queensland: Port Denison, BMNH 1984.12.24.36.

Victoria (Pliocene): Jimmy's Point Farm, coll. Maplestone. NMV T1757. (Last three samples and holotype listed under *S. hexagonalis* by Cook & Chimonides, 1987: 948).

Description

Colonies 10–11 mm when sexually mature. Autozooids with oval or suboval opesia, proximal edge sometimes almost straight; cryptocyst finely serrated. Operculum dark, placed above the distal half of the opesia. Subperipheral brooding zooids large, raised distally. Peripheral male zooids with elongated oval or pyriform opesia; subopercular tubercle absent. Avicularian shield with 14–20 fine bars, fused medially; frontal area narrowing distally, flanked by cryptocystal margins of adjacent zooids; condyle system reflexed.

Etymology

Verconis, L., genitive singular of Verco (construing the surname as a noun of the Third Declension); named after Dr Sir Joseph Cooke Verco (1851–1935).

Distribution

Known from south-western Western Australia (King George Sound), South Australia (Gulf St Vincent) and eastern Queensland, 2.5–192 m, and as a fossil from the Pliocene of Victoria.

Remarks

When redescribing *S. hexagonalis*, Cook & Chimonides (1987) noted the wide range of character states shown by both Maplestone's specimens and those in the BMNH, concluding that two partly sympatric forms might be involved. The four colonies from Western Australia examined here, some of which were collected with *S. hexagonalis* s. s., have the unequivocal character correlations of the Queensland specimens. This indicates, as previously suspected, that two distinct and sympatric species are present, one (*S. hexagonalis*) with a restricted distribution the other (*S. verconis*) with a wider geographical range and a fossil record.

S. verconis most resembles *S. hexagonalis* Maplestone, differing by its less robust zoaria, smaller and proportionately longer zooids with oval to suboval opesiae and more distal opercula, and by the avicularia having 14–20 fine bars (vs 12–16

stout bars in *S. hexagonalis*) and a more reflexed condyle system (see Fig. 1B).

'Selenaria' alata auctt.

Selenaria alata: Cook & Chimonides, 1985c: 339, figs 1, 2, 5, 9, 11–13 (Recent material only). *Non Selenaria alata* Tenison-Woods, 1880: 11, pl. 2, figs 12a–c.

Material Examined

South Australia: 35 Nm (64 km) SW of the North Neptunes, 104 fms (190 m), i.1905, SAM L597(3); no data, SAM L598(1).

Distribution

Known previously only from Bass Strait, 46–95 m. The present material adds South Australia to the recorded range of the species, and increases the lower depth-limit to 190 m.

Remarks

Of the four colonies examined, one was alive when collected. This species is characterized by its large, asymmetrical, unfused avicularian condyles and large trifoliate autozooidal opesia.

The Recent colonies from Bass Strait were all regenerated from fragments, and differed slightly from fossil *S. alata* in their less trifoliate autozooid opesia. The present specimens do not exceed 12 mm in diameter, and two have mandibles resembling those of *Otionella squamosa*, see Cook & Chimonides (1985c, fig. 11). The ancestrulae are all worn or partly obscured, but do not appear to be as large as those of the fossil colonies. The autozooidal opesia resemble those of the Bass Strait population, and are only slightly trifoliate. The somewhat ambiguous character of Recent *S. alata* auctt., which shares features with both fossil *S. alata* and *S. lata*, will be discussed in a later article (Bock & Cook in prep.). The character of the avicularian condyles and mandibles of *S. lata*, *S. alata* and *S. alata* auctt., together with the absence of zones of distinctive brooding and male zooids, means that none of these three species can be referred to *Selenaria* s. s., and they require a generic grouping of their own.

DISCUSSION

The present collections, though sparse in comparison with those previously reported from Bass Strait and New Zealand (Cook & Chimonides, 1987 and references therein; Nelson *et al.* 1988), are nevertheless significant in that they allow a first estimate of the diversity of the Selenariidae occurring in southern Western Australia and South Australia. The 16 species listed constitute a fairly

diverse fauna, comparable to that of Bass Strait with its 18 species. New State records are: Western Australia: *Selenaria bimorphocella*, *S. concinna*, *S. hexagonalis* and *S. verconis*; South Australia: *Otionella nitida*, *O. australis*, *S. punctata*, *S. concinna*, *S. varians*, *S. exasperans*, *S. verconis* and '*S. alata* auctt. Whereas most of the new locality records constitute only minor range-extensions (e.g. *S. concinna*), the extension in some cases is considerable. For example, *Helixotionella spiralis*, *H. scutata* and *S. pulchella*, previously known in the Recent only from the Jurien Bay district of Western Australia, are reported from the Eucla district of the Great Australian Bight, some 1 700 km to the south-east. Sufficient samples have now been analyzed from Bass Strait to permit the suggestion that these last three species are today genuinely absent from that region (though *H. spiralis* and *S. pulchella* have a fossil record in Victoria), and that the Great Australian Bight may well mark the eastern limit of their modern distribution. In addition, *S. hexagonalis* is reported from the Albany district of Western Australia, over 2 000 km west of its previous western limits in South Australia, and *S. varians* and *S. exasperans* are shown to occur at St Francis I., 1 000 km west of their original localities in Bass Strait (with *S. exasperans* occurring also at the intermediate localities of Cape Jaffa and Beachport in south-eastern South Australia).

The distribution of the species-pair *S. punctata* and *S. parapunctata* is of particular interest. The former is now known from most parts of the Australian continental shelf except Bass Strait, the Northern Territory and northern Queensland. Its absence from relatively well-collected Bass Strait may be real; moreover, in Bass Strait it appears to be replaced by *S. parapunctata*, which so far has not been reported from elsewhere.

Of the 18 species currently known from Bass Strait, seven are still notably absent from collections made further west: these are *Otionella minuta*, *O. auricula*, *Selenaria initia*, *S. minor*, *S. maculata*, *S. kompsaia*, and *S. maplestonei* (see Cook & Chimonides, 1985a, b; 1987). It is possible that at least some of these will eventually be found in South Australia and Western Australia. After the discovery of living *H. spiralis*, *S. pulchella*, *S. initia* and *S. minor* (originally described as fossils), it is possible that, with further collecting, other fossil species will also be discovered to be extant.

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A CHECKLIST OF HELMINTH PARASITES OF AUSTRALIAN AMPHIBIA

DIANE P. BARTON

Summary

This checklist includes all original references, and any other references which do more than repeat original work, of helminths occurring in Australian amphibians published up to 1992. Museum listings are also included, where available. Most records pertain to free-ranging animals; where they do not, they have been annotated appropriately.

A CHECKLIST OF HELMINTH PARASITES OF AUSTRALIAN AMPHIBIA

DIANE P. BARTON

BARTON, D. P. 1994. A checklist of helminth parasites of Australian Amphibia. *Rec. S. Aust. Mus.* 27(1): 13–30.

This checklist includes all original references, and any other references which do more than repeat original work, of helminths occurring in Australian amphibians published up to 1992. Museum listings are also included, where available. Most records pertain to free-ranging animals; where they do not, they have been annotated appropriately.

Helminths are arranged as follows: Monogenea, Digenea, Cestoda, Nematoda, Acanthocephala, in both the parasite-host and host-parasite checklists.

Hosts are presented by family with consideration given to recent taxonomic changes.

D. P. Barton, Zoology Department, James Cook University, Townsville, Queensland, Australia, 4811.
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INTRODUCTION

In 1939 May Young produced a checklist of helminth parasites recorded from Australian hosts. Thirteen amphibian hosts, infected with a total of 30 helminth species, were included. There has been no further compilation of solely Australian records from amphibians since then. The aim of this work is to produce an updated checklist of amphibian helminth parasites in Australia.

Included in this checklist are all original references, and any other references which do more than repeat original work, published up to 1992. Museum collections of amphibian parasites are also included, where available. Most records pertain to free ranging animals; where they do not, they have been annotated appropriately (e.g. experimental).

Comments on host taxonomy

Host names used in this checklist follow Cogger (1992), with the following exceptions:

i) *Kyarranus* Moore, 1958 is accepted as a valid genus (see Frost 1985).

ii) *Litoria pearsoniana* (Copland, 1961) is accepted as a valid species (see Frost 1985).

In the parasite-host checklist, host names are given as they were listed in the original publications. In the host-parasite checklist, the names have been updated to those used by Cogger (1992). The original names are also given with reference to the new name when there is an element of confusion.

All species formerly referred to the family Leptodactylidae are now placed in the family Myobatrachidae (see Cogger 1992).

All *Hyla* species are now referred to the genus *Litoria* (see Cogger 1992).

Limnodynastes dorsalis and *L. d. dumerilii*

recorded from South Australia, Queensland and New South Wales are referred to *L. dumerilii*. *Limnodynastes dorsalis* is only present in Western Australia (see Cogger 1992).

Litoria aurea and *L. a. raniformis* recorded from South Australia, Victoria and Tasmania are referred to *L. raniformis* (see Cogger 1992).

Litoria aurea recorded from Western Australia is referred to *Litoria* spp., as the range of *L. aurea* does not extend to Western Australia (see Cogger 1992).

Crinia sp. recorded from the Flinders Ranges, South Australia, in the Australian Helminthological Collection (AHC) list are most likely *C. riparia*. A group of these frogs was collected from Warren Gorge, which is within the range of *C. riparia* (Dr Margaret Davies, pers. comm.). A more precise geographical location is, however, required to differentiate *C. riparia* from *C. signifera*, so they must remain *Crinia* sp.

Litoria jervisiensis recorded from South Australia is referred to *L. ewingii* (see Cogger 1992).

Mixophyes sp. collected from the Bunya Mts, Queensland (AHC 6172), could be either *M. fasciolatus* or *M. iteratus*. Examination of the host specimen would be needed to determine the exact species.

Uperoleia marmorata collected from New England National Park, New South Wales (AHC 8055), could be either *U. rugosa* or *U. laevigata*. Davies & Littlejohn (1986) showed both species to be present in this region, while *U. marmorata* was restricted to the north-west of Western Australia. All *U. marmorata* in this checklist are from eastern Australia and helminths from these host specimens are referred to *Uperoleia* spp. Again, examination of the host specimen would be needed to determine which species is correct.

Bufo marinus was introduced to Australia in 1935

from South America (via Hawaii) (Easteal 1981). It is 'naturally' found in Queensland, northern New South Wales and eastern Northern Territory. Any locations recorded out of this range are from laboratory animals acquired from a commercial supplier.

Records of helminths from frogs in New Guinea are included only if that frog species is also found in Australia.

Comments on helminth taxonomy

Helminth nomenclature follows Prudhoe & Bray (1982) for Monogenea, Digenea and Cestoda, the CIH Keys to the Nematode Parasites of Vertebrates (Hartwich 1974; Chabaud 1975a, 1975b, 1978; Anderson & Bain 1976, 1982; Petter & Quentin 1976; Durette-Desset 1983) and Spencer Jones & Gibson (1987) for the Nematoda, and Amin (1985) for the Acanthocephala.

The taxonomic status of many genera and species infecting amphibians is in need of revision. Generally, original records of helminths are treated as correct, unless it is known to the author that appropriate revision has taken place.

All helminths are recorded in the parasite-host checklist under the current name with any synonyms also listed.

All previous records of lung nematodes from Australian frogs have been referred to *Rhabdias hylae* Johnston & Simpson, 1942, by Ballantyne (1971), a view accepted in this checklist.

Nasir & Diaz (1971) synonymised the Australian representatives of the genus *Mesocoelium* as *M. megaloon* Johnston, 1912, and *M. monas* (Rudolphi, 1819), Teixeira de Freitas, 1958 (*M. microon* Nicoll, 1914, *M. mesembrinum* Johnston, 1912, *M. oligoon* Johnston, 1912). This is not accepted here, pending further work on the genus.

Frogs often serve as an intermediate host for cestodes, being infected with plerocercoids/spargana in the musculature. The identification of this life cycle stage is impossible without knowledge of the definitive host. In other groups (Acanthocephala, Digenea), larval stages are often identifiable.

Explanation of Format

This checklist has been compiled from all published records up to 1992 known to the author, and from lists of museum holdings.

References to Prudhoe & Bray (1982) on microfiche are shown as 'mf' following the page number.

The lists are arranged as follows:

1. Parasite species are arranged systematically. The

amphibian hosts are listed for each helminth followed by the state or territory of origin (? denotes the state or territory was not referred to), literature references, and museum collection numbers, where available. The hosts are arranged with the type host first and all others listed alphabetically after.

2. Host species are arranged alphabetically within each family. The helminths from each host species are listed below the host with the phase of development and site of infection recorded, where known.

3. References.

Authors whose names appear frequently are referred to, where appropriate, by initials, as follows:

LMA L. Madeline Angel
MRY May R. Young
PMM Patricia M. Mawson
SJJ Stephen J. Johnston
THJ T. Harvey Johnston

The major helminth parasite groups are referred to by their initials:

M Monogenea
D Digenea
C Cestoda
N Nematoda
A Acanthocephala

Museums and other sources which are referred to as having amphibian parasites in their collection are abbreviated as follows:

AHC Australian Helminthological Collection, (in the South Australian Museum) Adelaide, SA
AM Australian Museum, Sydney, NSW
BM(NH) Natural History Museum, London, England
CAS Institute of Parasitology, Czechoslovak Academy of Sciences, České Budejovice, Czechoslovakia
QM Queensland Museum, Brisbane, Qld
SAM South Australian Museum, Adelaide, SA
SP Personal collection of Ms Sylvie Pichelin, Parasitology Department, University of Queensland, Brisbane, Qld
TM Tasmanian Museum and Art Gallery, Hobart, Tas

State names are abbreviated as follows:

NSW New South Wales
NT Northern Territory
Qld Queensland
SA South Australia, including Kangaroo I. & Pearson I.

Tas	Tasmania, including Bass Strait Islands (King & Flinders)
Vic	Victoria
WA	Western Australia

ORDER AND ARRANGEMENT OF PARASITES AS PRESENTED
UNDER EACH HOST

1. **Phylum Platyhelminthes**

Class Monogenea Carus, 1863
Order Polyopisthocotylea Odhner, 1912

Family POLYSTOMATIDAE Carus, 1863,
emended Gamble, 1896
Subfamily Polystomatinae Gamble, 1896

Class Trematoda Rudolphi, 1808
Order Digenea Van Beneden, 1858
Suborder Prosostomata Odhner, 1905

Family PARAMPHISTOMATIDAE Fiscoeder,
1901
Subfamily Diplodiscinae Cohn, 1904
Family GORGODERIDAE Looss, 1901
Family ALLOCREADIIDAE Stossich, 1903
Family PLAGIORCHIIDAE Lühe, 1901,
emended Ward, 1917
Subfamily Haematoloechinae Teixeira de Freitas
& Lent, 1939, emended Yamaguti, 1958
Family TELORCHIIDAE Stunkard, 1924
Subfamily Opisthioglyphinae Dollfus, 1949
Family BRACHYCOELIIDAE Johnston, 1912
Family LECITHODENDRIIDAE Odhner, 1910
Family BRACHYLAIMIDAE Joyeux & Foley,
1930
Family DIPLOSTOMIDAE Poirier, 1886
Family DOLICHOPELIDAE Yamaguti, 1971

Not further identified

Class Cestoidea Rudolphi, 1808
Order Pseudophyllidea Carus, 1863
Family DIPHYLLOBOTHRIIDAE Lühe, 1910

Order Proteocephalidea Mola, 1928
Family PROTEOCEPHALIDAE La Rue, 1911

Order Cyclophyllidea Braun, 1900
Family NEMATOTAENIIDAE Lühe, 1910

Not further identified

2. **Phylum Nematoda**

Class Secernentea
Order Rhabditida
Superfamily Rhabditoidea
Family RHABDIASIDAE Railliet, 1916

Order Strongylida
Superfamily Trichostrongyloidea
Family MOLINEIDAE (Skrjabin & Schulz, 1937)
Durette-Desset & Chabaud, 1977

Order Oxyurida
Superfamily Oxyuroidea
Family PHARYNGODONIDAE Travassos, 1919

Order Ascaridida
Superfamily Cosmocercidae
Family COSMOCERCIDAE (Railliet, 1916,
subfam.) Travassos, 1925
Superfamily Ascaridoidea
Family ASCARIDIDAE Baird, 1853

Order Spirurida
Superfamily Physalopteroidea
Family PHYSALOPTERIDAE (Railliet, 1893,
subfam.) Leiper, 1908
Superfamily Habronematoidea
Family HEDRURIDAE Railliet, 1916
Superfamily Filarioidea

Not further identified

3. **Phylum Acanthocephala**

Class Palaeacanthocephala Meyer, 1931
Order Echinorhynchida Southwell & MacFie, 1925
Family ECHINORHYNCHIDAE Cobbold, 1876

Order Polymorphida Petrochenko, 1956
Family PLAGIORHYNCHIDAE Golvan, 1960

Not further identified

ORDER AND ARRANGEMENT OF HOSTS AS PRESENTED IN
HOST-PARASITE CHECKLIST

Class Amphibia
Order Anura
Family MYOBATRACHIDAE
Adelotus
Arerophryne

Assa
Crinia
Geocrinia
Heleioporus
Hyperoleia
Kyarranus
Leptodactylid
Limnodynastes
Metacrinia
Mixophyes
Myobatrachid
Neobatrachus
Paracrinia
Phyloria
Pseudophryne
Ranidella
Rheobatrachus
Taudactylus
Uperoleia
 Family HYLIDAE
Chiroleptes
Cyclorana
Hyla
Litoria

Family RANIDAE
Rana

Family BUFONIDAE
Bufo

Unidentified Anura

PARASITE-HOST CHECKLIST

1. Phylum Platyhelminthes

Class Monogenea Carus, 1863

Order Polyopisthocotylea Odhner, 1912

Family POLYSTOMATIDAE Carus, 1863,
 emended Gamble, 1896
 Subfamily Polystomatinae Gamble, 1896

Parapolystoma bulliense (Johnston, 1912),
 Ozaki, 1935

syn. *Polystomum bulliense* Johnston, 1912
Hyla phyllochroa, NSW, SJJ 1912: 297, AM
 W.346, QM GL 12109, GL 12160, AHC 2200
 (wholemound), 2217–2219 (sections)
Hyla lesueurii, NSW, SJJ 1912: 297
Litoria citropa, NSW, AHC 5167
Litoria pearsoniana, Qld, SP

Parapolystoma sp.
Litoria nyakalensis, Qld, SP

Class Trematoda Rudolphi, 1808

Order Digenea Van Beneden, 1858

Suborder Prosostomata Odhner, 1905

Family PARAMPHISTOMATIDAE Fischeoeder,
 1901

Subfamily Diplodiscinae Cohn, 1904

Diplodiscus megalochrus Johnston, 1912
Hyla aurea, NSW, SJJ 1912: 302, AM W.332,
 QM GL 11851
 Frog, NSW, AHC 3310
Hyla caerulea, Qld, THJ 1916b: 60
Limnodynastes peronii, NSW, SJJ 1912: 302
Litoria caerulea, Qld, Prudhoe & Bray 1982:
 199 mf

Diplodiscus microchrus Johnston, 1912
Hyla ewingii, NSW, SJJ 1912: 307, AM W.333
Limnodynastes tasmaniensis, NSW, SJJ 1912:
 307

Diplodiscus sp.
Bufo marinus, Qld, AHC 14, 2978, 3028,
 3553, 3563, 3576, 3875
Hyla aurea, NSW, AHC 12683
Hyla caerulea, Qld, QM GL 12350

Amphistome

Bufo marinus, Qld, AHC 4944

Distoma sp.

Hyla aurea, ?, MRY 1939: 74

Family GORGODERIDAE Looss, 1901

Gorgoderia australiensis Johnston, 1912
Hyla aurea, NSW, SJJ 1912: 326, AM
 W.340a, AM W. 395, AM W.19850, QM GL
 11860, GL 12161
Limnodynastes dorsalis, SA, AHC 3511
Limnodynastes peronii, NSW, SJJ 1912: 326,
 AM W.340 (this number is given for *H. aurea*
 in SJJ 1912: 326, but in AM records is for *L.*
peronii)

Gorgoderia sp.

Hyla aurea, NSW, AHC 12680; Vic, AHC
 4539; SA, AHC 3529, 3532
Limnodynastes dorsalis, SA, AHC 3498, 3502,
 12698
Limnodynastes tasmaniensis, SA, AHC 3489

Family ALLOCREADIIDAE Stossich, 1903

Allocreadiidae sp.

Cyclorana cultripis, Qld, QM GL 11285

Family PLAGIORCHIIDAE Lühe, 1901,
 emended Ward, 1917

Subfamily Haematoleochinae Teixeira de Freitas
 & Lent, 1939, emended Yamaguti, 1958

Haematoleochus australis (S.J. Johnston, 1912),
 Inglis, 1932 syn. *Pneumonoeces australis* S.J.
 Johnston, 1912

Hyla aurea, NSW, SJJ 1912: 321, AM W.339,
 W.339a, W.396, W.19849; ?, QM GL 11868,
 GL 1197

- Limnodynastes peronii*, NSW, SJJ 1912: 321
Litoria aurea, Tas, AHC 5404
Litoria moorei, WA, Prudhoe & Bray 1982: 83 mf, BM(NH) 1967.10.23.7–9
- Family TELORCHIIDAE Stunkard, 1924
 Subfamily Opisthioglyphinae Dollfus, 1949
- Dolichosaccus anartius*** (S.J. Johnston, 1912)
 Yamaguti, 1958
 syn. *Brachysaccus anartius* S.J. Johnston, 1912
Hyla aurea, NSW, SJJ 1912: 317, AM W.337, W.398, QM GL 11846, AHC 12685, 12686; ?, QM GL 11868, GL 11997
Limnodynastes peronii, NSW, SJJ 1912:317
- Dolichosaccus diamesus*** S.J. Johnston, 1912
Hyla freycineti, NSW, SJJ 1912: 315, AM W.336, W.19848
- Dolichosaccus ischyryus*** S.J. Johnston, 1912
Limnodynastes dorsalis, NSW, SJJ 1912: 314, AM W.335
Hyla caerulea, NSW, SJJ 1912: 314; Qld, THJ 1916: 60
- Dolichosaccus juvenilis*** (Nicoll, 1918),
 Travassos, 1930
 syn. *Brachysaccus juvenilis* Nicoll, 1918
Chiroleptes brevipalmatus, Qld, Nicoll 1918: 368
Cyclorana cultripes, Qld, QM GL 11280
- Dolichosaccus symmetrus*** (S.J. Johnston, 1912),
 Yamaguti, 1958
 syn. *Brachysaccus symmetrus* Johnston, 1912
Hyla caerulea, NSW, SJJ 1912: 319, AM W.338
Bufo marinus, Qld, AHC 13
- Dolichosaccus trypheryus*** S.J. Johnston, 1912
Limnodynastes peronii, NSW, SJJ 1912: 310, AM W.334, QM GL 11850
Hyla aurea, NSW, SJJ 1912: 310, QM GL 11850; SA, AHC 12704
Limnodynastes dorsalis, SA, AHC 12699
Limnodynastes tasmaniensis, SA, AHC 3485, 3487, 3488
Litoria moorei, WA, BM(NH) 1968.4.19.16
- Dolichosaccus* sp.**
 syn. *Brachysaccus* sp.
Bufo marinus, Qld, AHC 18, 2973, 2975, 3559, 3874, 4952, 4953, 5192
Hyla aurea, NSW, AHC 3527, 12682
Hyla caerulea, Qld, AHC 12690
Hyla sp., ?, MRY 1939: 75
Limnodynastes dorsalis, SA, AHC 3512, 3513, 12677
Limnodynastes fletcheri, SA, AHC 4583
Limnodynastes tasmaniensis, SA, AHC 3485, 3487, 3488
- Family BRACHYCOELIIDAE Johnston, 1912
- Mesocoelium megaloon*** S.J. Johnston, 1912
Hyla ewingii, NSW, SJJ 1912: 335, AM W.343
Litoria caerulea, ?, Freitas 1963: 179 (noted that this specimen should be *M. mesembrinum*)
Litoria ewingii, ?, Prudhoe & Bray 1982:117 mf
- Mesocoelium mesembrinum*** S.J. Johnston, 1912
Hyla caerulea, NSW, SJJ 1912: 330, AM W.341, W.341b, W.393, W.394, AHC 4538
Bufo marinus, Qld, Yuen 1965: 271
Litoria aurea, ?, Prudhoe & Bray 1982: 117
Litoria caerulea, Qld, THJ 1916b: 60; NSW, QM GL 11861
- Mesocoelium microon*** Nicoll, 1914
Litoria caerulea, Qld, Nicoll 1914: 339, QM GL 11131
Cyclorana cultripes, Qld, QM GL 11278
Litoria gracilentia, Qld, Nicoll 1914: 339, QM GL 11169
- Mesocoelium oligoon*** S.J. Johnston, 1912
Hyla citropus, NSW, SJJ 1912: 336 AM W.342
- Mesocoelium* sp.**
Bufo marinus, Qld, Freeland et al. 1986: 496, AHC 16, 17, 2967, 2973, 2975, 3138, 3876, 4949, 4951, 4955; SA, AHC 4547
 (*Mesocoelium* sp. 2 of LMA)
Hyla caerulea, Qld, AHC 3517–3521, 3523, 3524
- Family LECITHODENDRIIDAE Odhner, 1910
- Pleurogenoides freycineti*** (S.J. Johnston, 1912),
 Travassos, 1930
 syn. *Pleurogenes freycineti* Johnston, 1912
Hyla freycineti, NSW, SJJ 1912: 342, AM W.344
- Pleurogenoides solus*** (S.J. Johnston, 1912),
 Travassos, 1930
 syn. *Pleurogenes solus* Johnston, 1912
Hyla aurea, NSW, SJJ 1912: 345, AM W.345, W.19851, W.19852
- Pleurogenes* spp.**
Hyla spp., ?, MRY 1939: 75
- Lecithodendriid* sp.**
Bufo marinus, Qld, Freeland et al. 1986: 496
- Family BRACHYLAIMIDAE Joyeux & Foley, 1930
- Zeylanurotrema spearei*** Cribb & Barton, 1991
Bufo marinus, Qld, Cribb & Barton 1991: 207, QM GL 1273, 1274–76, AHC 18984, BM(NH) 1990.12.7.3–5
- Family DIPLOSTOMIDAE Poirier, 1886
- Fibricola intermedius*** (Pearson, 1959),

Sudarikov, 1961

syn. *Neodiplostomum intermedium* Pearson, 1959

Hyla pearsoni, ?, diplostomula, Pearson 1961: 135

Hyla caerulea, paratenic host, ?, Pearson 1961: 136

Hyla latopalmata tadpole, ?, Pearson 1961: 135

Leptodactylid sp., ?, Pearson 1961: 135

Mixophyes fasciolatus tadpole, ?, Pearson 1961: 135

Family DOLICHOPELIDAE Yamaguti, 1971

Dolichopeloides macalpini (Nicoll, 1918),

Johnston & Angel, 1940

syn. *Dolichopeloides macalpini* Nicoll, 1918

Limnodynastes sp. tadpole, SA, metacercaria, THJ & Angel 1940: 381, AHC 201320

Hyla aurea raniformis, SA, metacercaria, THJ & Angel 1940: 382

Limnodynastes dorsalis (*dumerili*), SA, metacercaria, THJ & Angel 1940: 382

Limnodynastes tasmaniensis (*platycephalus*), SA, metacercaria, THJ & Angel 1940: 382

Tadpole, SA, metacercaria, AHC 2725

Digenea Not Further Identified

Cercaria ameriannae T.H. Johnston & Beckwith, 1947

Limnodynastes sp., SA, diplostomula, (experimental), THJ & Beckwith 1947: 578, AHC 20219

Tadpole, SA, diplostomula, (experimental), AHC 2272

Cercaria angelae T.H. Johnston & Simpson, 1944

Limnodynastes tasmaniensis tadpole, SA, cysts, AHC 2825; experimental infection of *L. tasmaniensis* tadpoles produced *Tetracotyle* cysts (THJ & Simpson 1944: 131)
Tadpole, SA, metacercaria, AHC 2829, cysts, AHC 2831, 2833

Cercaria ellisi T.H. Johnston & Simpson, 1944

Crinia signifera tadpole, SA, metacercaria, (experimental), THJ & Simpson 1944: 89
Tadpole, SA, cyst, AHC 20206

Cercaria lethargica T.H. Johnston & Muirhead, 1949

Tadpole, SA, AHC 2821

Cercaria natans T.H. Johnston & Muirhead, 1949

Limnodynastes tasmaniensis tadpole, SA, (experimental), THJ & Muirhead, 1949: 104 (belongs to *Echinostomum* group); AHC 12402

Cercaria sp.

Tadpole, SA, (K.I. stylet: experimental), AHC 20260 (*Echinostome* J: experimental), AHC

20261

(Stylet J.W.: experimental), AHC 20262

Diplostomula

Hyla aurea, SA, AHC 12390

Hyla peronii, SA, AHC 12838

Limnodynastes sp., SA, (experimental), AHC 12398

Limnodynastes tasmaniensis, SA, AHC 4125, 4134, 12702

Echinostome cysts

Frog, SA, AHC 12712

Hyla aurea, SA, AHC 12713

Tadpole, SA, AHC 12387; (experimental), AHC 12722

Halipegus sp.

Litoria caerulea, NT, AHC 5405

Plagiorchid cysts

Hyla aurea, SA, AHC 12388

Strigeid cysts

Hyla aurea, SA, AHC 12384, 12386, 12394

Limnodynastes tasmaniensis, SA, AHC 12380

Tetracotyle cysts

Hyla aurea, SA, AHC 12382

Digenea cysts

Bufo marinus, Qld, cysts, Freeland et al. 1986: 494

Frog, NSW, cysts, AHC 12393

Hyla aurea, NSW, cysts, AHC 12372, 12373, 12390, 12392, 12718–12721

Hyla peroni, SA, cysts, AHC 12401

Limnodynastes dorsalis, SA, cysts, AHC 12369, 12385, 12400, 12406, 12407

Limnodynastes tasmaniensis, SA, cysts, AHC 12370, 12371, 12389, 12395, 12397, 12399, 12406, 12407

Tadpole, SA, cysts, AHC 12375–12377, 12403; (experimental), AHC 12379

Digenea

Bufo marinus, Qld, Freeland et al. 1986: 496; Qld, AHC 15, 19, 2004, 2969, 2971, 2977, 3145, 3157, 3309, 3313, 3535–3552, 3555–3558, 3561, 3562, 3564–3575, 3577–3580, 3880, 3947, 4077, 4078, 4099, 4101, 4215, 4351, 4889, 5020, 5021

Hyla aurea, NSW, AHC 12687, 12681, 4546, 4537, 4536, 4535; SA, AHC 3520, 4083, 4341, 4579, 12688

Hyla peroni, SA, AHC 12396

Limnodynastes dorsalis, SA, AHC 3494–3497, 3499–3501, 3504–3510, 4545, 4548–4550, 12676, 12700

Limnodynastes fletcheri, SA, AHC 12678

Limnodynastes sp., SA, AHC 3478–3480, 3482, 3483

Limnodynastes tasmaniensis, SA, AHC 1877, 3484

Litoria caerulea, Qld, AHC 3522, 3525, 3526, 12691; NT, AHC 4544

Litoria dahlii, NT, AHC 6809, 6993
Litoria moorei, WA, AHC 8545
Litoria rothii, Qld, AHC 7181
Rheobatrachus silus, Qld, AHC 6232
Taudactylus diurnus, Qld, AHC 8237

Class Cestoidea Rudolphi, 1808
Order Pseudophyllidea Carus, 1863

Family DIPHYLLOBOTHRIIDAE Lühe, 1910

?*Ligula* sp.

Hyla aurea, NSW, larval stage, Haswell 1890: 661 (recorded as having possible affinities with *Ligula*)
Hyla caerulea, Qld, AHC 2350–2352

Spirometra erinacei Rudolphi, 1819

Litoria rubella, NT, AHC 17857

Diphyllbothriidae spargana

(?*Diphyllbothrium* (= *Spirometra*) *erinacei* (Rudolphi, 1819))

Bufo marinus, Qld, AHC 4100
Hyla aurea, NSW, WA, THJ 1912: 70
Hyla caerulea, Qld, NSW, THJ 1912: 70
Hyla latopalmata, ?, (experimental), Sandars 1953: 67
Hyla latopalmata tadpole, ?, (experimental), Sandars 1953: 67

? ***Spirometra masoni*** (Cobbold, 1882), Stiles & Taylor, 1902 *Bufo marinus*, spargana, Bennett 1978: 756

Order Proteocephalidea Mola, 1928

Family PROTEOCEPHALIDAE La Rue, 1911

***Ophiotaenia* sp.**

Hyla aurea, ?, SJJ 1914: 44; SA, AHC 2825

Proteocephalus hylae (S.J. Johnston, 1912), Prudhoe & Bray, 1982

syn. *Ophiotaenia hylae* S.J. Johnston, 1912

Hyla aurea, NSW, THJ 1912: 63
Litoria aurea, NSW, QM G 423
Litoria moorei, WA, BM(NH) 1968.4.19.1–5; AHC 8178

Proteocephalid plerocercoids

Bufo marinus, Qld, Freeland et al. 1986: 496
Crinia laevis, Tas, Hickman 1960: 20
Crinia signifera, Tas, Hickman 1960: 20
Hyla aurea, Vic, AHC 2327; SA, AHC 8696
Limnodynastes peronii, Tas, Hickman 1960: 20

Order Cyclophyllidea Braun, 1900

Family NEMATOTAENIIDAE Lühe, 1910

Cylindrotaenia crinia (Hickman, 1960), Jones, 1987

syn. *Baerietta crinia crinia* Hickman, 1960
Crinia tasmaniensis, Tas, Hickman 1960: 18,

TM K710–712

Ranidella tasmaniensis, Tas, Jones 1987: 207
Cylindrotaenia minor (Hickman, 1960), Jones, 1987

syn. *Baerietta crinia minor* Hickman, 1960

Crinia tasmaniensis, Tas, Hickman 1960: 18
Crinia laevis, Tas, Hickman 1969: 18
Crinia signifera, Tas, Hickman 1960: 18; TM K716–717

Ranidella tasmaniensis, Tas, Jones 1987: 211
Assa darlingtoni, NSW, Jones 1987: 212, QM GL 4887; Qld, Jones & Delvinquier 1991: 492
Geocrinia laevis, Tas, Jones 1987: 211
Philoria loveridgei, Qld, Jones & Delvinquier 1991: 492

Ranidella signifera, Tas, Jones 1987: 211

Nematotaenia hylae Hickman, 1960

Hyla ewingii, Tas, Hickman 1960: 8, TM K705, K707–709

Litoria ewingii, Tas, Jones 1987: 184, 185
Bufo marinus, Qld, Jones & Delvinquier 1991: 492

Crinia signifera, Tas, Hickman 1960: 8, TM K706

Cyclorana novaehollandiae, Qld, Jones & Delvinquier 1991: 492

Limnodynastes ornatus, Qld, Jones & Delvinquier 1991: 492

Litoria fallax, Qld, Jones 1987: 185

Litoria inermis, Qld, Jones 1987: 185

Litoria latopalmata, Qld, Jones 1987: 185, QM GL 4886

Litoria pallida, Qld, Jones & Delvinquier 1991: 492

Litoria peronii, Qld, Jones & Delvinquier 1991: 492

Ranidella parinsignifera, Qld, Jones 1987: 185, QM GL 4887

Ranidella signifera, Tas, Jones 1987: 184, 185

Ranidella riparia, SA, Jones & Delvinquier 1991: 492

Uperoleia rugosa, Qld, Jones & Delvinquier 1991: 492

***Nematotaenia* sp.**

Hyla caerulea, ?, MRY 1939: 74; NSW, THJ 1916a: 195, Prudhoe & Bray 1982: 12 mf
Hyla freycineti, ?, MRY 1939: 75; NSW, THJ 1916a: 194, Prudhoe & Bray 1982: 12 mf
Hyperoleia marmorata, ?, MRY 1939: 75; NSW, THJ 1916a: 194, Prudhoe & Bray 1982: 12 mf

Triplotaenia mirabilis Boas, 1902

Hyla aurea, ?, MRY 1939: 74 (usually a cestode of marsupials; see Prudhoe & Bray 1982: 3 mf for discussion)

Cestoda Not Further Identified

Bufo marinus, Qld, AHC 10, 46, 4892
Crinia signifera, SA, AHC 4419, 4424, 20687
Crinia sp., SA, AHC 4234
Hyla aurea, NSW, SJJ 1912: 291; Vic, AHC 2326; SA, larva, AHC 4584
Hyla caerulea, NSW, SJJ 1912: 290; Qld, AHC 1223
Hyla ewingi, NSW, AHC 4082; SA, AHC 4304, 4369
Hyla ewingi alpina, NSW, AHC 4079–4081
Hyla freycineti, NSW, SJJ 1912: 291
Hyla sp., SA, AHC 40
Hyperoleia marmorata, NSW, SJJ 1912: 290
Limnodynastes sp., Qld, AHC 2376; SA, AHC 2378
Metacrinia nichollsi, WA, AHC 48
Rheobatrachus silus, Qld, AHC 8913
 Frog, SA, AHC 20678

2. Phylum Nematoda

Class Secernentea

Order Rhabditida

Superfamily Rhabditoidea

Family RHABDIASIDAE Railliet, 1916

Rhabdias australiensis Moravec & Sey, 1990
Rana daemeli, Qld, Moravec & Sey 1990: 283, CAS N-450

Rhabdias hylae Johnston & Simpson, 1942

Hyla aurea, NSW, THJ & Simpson 1942: 176, SJJ 1912: 291 (lung nematode); VIC, THJ & Simpson 1942: 176; SA, Ballantyne 1971: 51
Adelotus brevis, Qld, Ballantyne 1971: 51
Crinia georgiana, WA, Ballantyne 1971: 51
Crinia glauerti, WA, Ballantyne 1971: 51
Crinia insignifera, WA, Ballantyne 1971: 51
Crinia leai, WA, Ballantyne 1971: 51
Crinia signifera, NSW, SA, Ballantyne 1971: 50
Crinia subinsignifera, WA, Ballantyne 1971: 51
Crinia victoriana, Vic, Ballantyne 1971: 50
Hyla aurea raniformis, Vic, Ballantyne 1971: 50
Hyla caerulea, QLD, THJ & Simpson 1942: 176
Hyla latopalmata, Qld, Ballantyne 1971: 51
Hyla lesueuri, Qld, Ballantyne 1971: 51
Hyla peroni, NSW, SJJ 1912: 290 (lung nematode); THJ & Simpson 1942: 178
Limnodynastes dorsalis, NSW, THJ & Simpson 1942: 179
Limnodynastes fletcheri, Qld, Ballantyne 1971: 51
Limnodynastes peroni, NSW, SJJ 1912: 290 (lung nematode); THJ & Simpson 1942: 179;

Qld, Ballantyne 1971: 51; SA, Ballantyne 1971: 51

Limnodynastes tasmaniensis, NSW, SJJ 1912: 290 (lung nematode), THJ & Simpson 1942: 176; SA, THJ & Simpson 1942: 176, Ballantyne 1971: 50; Vic, Ballantyne 1971: 50
Mixophyes fasciolatus, Qld, Ballantyne 1971: 51

Pseudophryne bibronii, NSW, Ballantyne 1971: 50

Pseudophryne guentheri, WA, Ballantyne 1971: 51

Pseudophryne occidentalis, WA, Ballantyne 1971: 51

Pseudophryne sp., SA, Ballantyne 1971: 51

Rhabdias nigrovenosum (Goeze, 1800)

syn. *Rhabdonema nigrovenosum* Goeze, 1800; listed as a synonym of *Rhabdias bufonis* (Schrank, 1788) in Yamaguti 1961: 84

Hyla aurea, ?, AM W.19853–6

Rhabdias sp.

Hyla aurea, NSW, VIC, THJ & Simpson 1942: 178 (referring to THJ 1938: 151); WA, BM(NH) 1989.1987–1988

Hyla moorei, WA, BM(NH) 1980.263–282

Rhabdonema sp.

Hyla aurea, NSW, Vic, THJ & Simpson 1942: 178 (referring to Haswell 1891)

Hyla caerulea, QLD, THJ 1916b: 60

Order Strongylida

Superfamily Trichostrongyloidea

Family MOLINEIDAE (Skrjabin & Schulz, 1937) Durette-Desset & Chabaud, 1977

Oswaldocruzia (O.) *limnodynastes* T.H.

Johnston & Simpson, 1942

Limnodynastes dorsalis, SA, THJ & Simpson 1942: 172; THJ & PMM 1949: 65

Hyla aurea, NSW, Vic, THJ & Simpson 1942: 172

Hyla peroni, SA, THJ & PMM 1949: 65

Order Oxyurida

Superfamily Oxyuroidea

Family PHARYNGODONIDAE Travassos, 1919

Parathelandros australiensis (Johnston & Simpson, 1942), Inglis, 1968

syn. *Cosmocerca australiensis* Johnston & Simpson, 1942

Limnodynastes dorsalis, SA, THJ & Simpson 1942: 176

Limnodynastes fletcheri, SA, Inglis 1968: 173

Parathelandros carinae Inglis, 1968

- Heleioporus albopunctatus*, WA, Inglis 1968: 176
Heleioporus australiacus, WA, Inglis 1968: 176
Heleioporus eyrei, WA, Inglis 1968: 176
Heleioporus psammophilus, WA, Inglis 1968: 176
Neobatrachus pelobatoides, WA, Inglis 1968: 176
- Parathelandros johnstoni*** Inglis, 1968
Heleioporus eyrei, WA, Inglis 1968: 175
Limnodynastes dorsalis, WA, Inglis 1968: 175
Neobatrachus centralis, WA, Inglis 1968: 175 (specimens in poor condition, may be *P. maini* or *P. limnodynastes*)
Neobatrachus pelobatoides, WA, Inglis 1968: 175
- Parathelandros limnodynastes*** (Johnston & Mawson, 1942), Inglis, 1968
 syn. *Pharyngodon limnodynastes* Johnston & Mawson, 1942
Limnodynastes dorsalis, SA, THJ & PMM 1942: 94; Inglis 1968: 175
Limnodynastes dorsalis dumerili, SA, THJ & PMM 1942: 94
- Parathelandros maini*** Inglis, 1968
Hyla moorei, WA, Inglis 1968: 176
Hyla adelaidensis, WA, Inglis 1968: 176
Hyla cyclorhyncha, WA, Inglis 1968: 176
- Parathelandros mastigurus*** Baylis, 1930
Hyla caerulea, Qld, Baylis 1930: 359, Inglis 1968: 173; NSW, Inglis 1968: 173
Bufo marinus, Qld, Inglis 1968: 173
Hyla gracilentia, Qld, Baylis 1930: 359
Hyla gracilis, Qld, Inglis 1968: 173 (refers to *Hyla gracilentia* recorded by Baylis 1930)
- Parathelandros propinqua*** (Johnston & Simpson, 1942), Inglis, 1968
 syn. *Cosmocerca propinqua* Johnston & Simpson, 1942
Limnodynastes dorsalis, SA, THJ & Simpson 1942: 176
- Parathelandros spp.***
Bufo marinus, Qld, Freeland et al. 1986: 496
Hyla aurea, WA, (female only), BM(NH) 1980.283–292
Hyla rubella, WA, (female only), BM(NH) 1980.318–317
 Oxyurids Not Further Identified
Bufo marinus, Qld, AHC 2276, 4950; Vic, AHC 9048, 9059
Cyclorana sp., NT, AHC 4450
Hyla aurea, Vic, AHC 2311
Hyla caerulea, Qld, AHC 2343; NT, AHC 4947
Limnodynastes dorsalis, SA, AHC 2306, 3176
Limnodynastes tasmaniensis, SA, AHC 1417, 5030
- Litoria rothii*, Qld, AHC 7156
Litoria rubella, Qld, AHC 7180
Mixophyes sp., Qld, AHC 6172
- Order Ascaridida
- Superfamily Cosmocercoidae
 Family COSMOCERCIDAE (Railliet, 1916 subfam.) Travassos, 1925
- Cosmocerca limnodynastes*** Johnston & Simpson, 1942
Limnodynastes dorsalis, SA, THJ & Simpson 1942: 174
- Cosmocercinae gen. sp. 1**
Rana daemeli, Qld, Moravec & Sey 1990: 273
- Austraplectana kartanum*** (Johnston & Mawson, 1941), Baker, 1981
 syn. *Rallietnema kartanum* Johnston & Mawson, 1941
Hyla jervisiensis, SA, THJ & PMM 1941: 146
Heleioporus eyrei, WA, Inglis 1968: 166
Hyla moorei, WA, Inglis 1968: 166, BM(NH) 1967. 1158–1159
Litoria nasuta, Qld, Baker 1981: 111
Austraplectana sp.
 Frog, Qld, Baker 1981: 116
- Maxvachonia adamsoni*** Moravec & Sey, 1990
Litoria infrafronata, New Guinea, Moravec & Sey 1990: 276, CAS N-449
- Maxvachonia ewersi*** Mawson, 1972
Litoria nasuta, New Guinea, PMM 1972: 105
- Maxvachonia flindersi*** (Johnston & Mawson, 1941), Mawson, 1972
 syn. *Aplectana flindersi* Johnston & Mawson, 1941; *Austracerca flindersi* (Johnston & Mawson, 1941) Inglis 1968
Hyla jervisiensis, SA, THJ & PMM 1941: 148
Bufo marinus, Qld, PMM 1972: 104, AHC 5170
Heleioporus australiacus, WA, Inglis 1968: 165
Heleioporus barycragus, WA, PMM 1972: 104
Heleioporus inornatus, WA, PMM 1972: 104, AHC 5180
Heleioporus psammophilus, WA, Inglis 1968: 165
Hyla cyclorhyncha, WA, Inglis 1968: 165
Limnodynastes dorsalis, SA, PMM 1972: 104, AHC 5183
Litoria adelaidensis, WA, PMM 1972: 104, AHC 5172
Litoria caerulea, NT, PMM 1972: 104, AHC 5182
Litoria moorei, WA, PMM 1972: 104, AHC 5175
- Falcaustra hylae*** (Johnston & Simpson, 1942), Chabaud & Golvan, 1957

syn. *Spironoura hylae* Johnston & Simpson, 1942
Hyla aurea, NSW, THJ & Simpson 1942: 173

Cosmocercoid

Bufo marinus, Qld, AHC 5009

Superfamily Ascaridoidea

Family ASCARIDIDAE Baird, 1853

Ophidascaris pyrrhus Johnston & Mawson, 1942
 Tadpole, Qld, (experimental infection), QM
 GL 9107

Frog, Qld, QM GZ 15

Raillietascaris varani (Baylis & Daubney, 1922),
 Sprent, 1985

Tadpole, ?, QM GL 5674

Seuratascaris numidica (Seurat, 1917), Sprent,
 1985

Rana daemeli, Qld, Sprent 1985: 241

Order Spirurida

Superfamily Physalopteroidea

Family PHYSALOPTERIDAE (Railliet, 1893
 subfam.) Leiper, 1908

Pseudorictularia disparilis (Irwin-Smith, 1922),
 Dollfus & Desportes, 1945

syn. *Rictularia disparilis* Irwin-Smith, 1922

Litoria inermis, Qld, Owen & Moorhouse
 1980: 1014

Litoria nigrofrenata, Qld, Owen & Moorhouse
 1980: 1014

Rana daemeli, Qld, Owen & Moorhouse 1980:
 1013

Physaloptera confusa T.H. Johnston & Mawson,
 1942

Limnodynastes tasmaniensis, NSW, encysted
 larva, THJ & Simpson 1942: 178; SA, encysted
 larva, THJ & PMM 1949:69

Hyla aurea, NSW, encysted larva, THJ &
 PMM 1942: 91; THJ & Simpson 1942: 178

Hyla caerulea, Qld, encysted larva, THJ &
 Simpson 1942: 178

Hyla peroni, SA, encysted larva, THJ & PMM
 1942: 91; THJ & PMM 1949: 69; THJ &
 Simpson 1942: 178

Limnodynastes dorsalis, SA, encysted larva,
 THJ & PMM 1942: 91; NSW, encysted larva,
 THJ & Simpson 1942: 178

Limnodynastes dorsalis dumerilii, SA,
 encysted larva, THJ & PMM 1942: 91; THJ &
 Simpson 1942: 178

Physaloptera sp.

Cyclorana australis, WA, larva AHC 6399

Heleioporus eyrei, WA, AHC 3012

Hyla aurea, SA, AHC 12386

Limnodynastes dorsalis dumerilii, SA, cysts,
 AHC 2356 (frog taken from intestine of tiger
 snake, *Notechis scutatus*), 2375

Superfamily Habronematoidea

Family HEDRURIDAE Railliet, 1916

Hedruris hylae Johnston & Mawson, 1941

Hyla jervisiensis, SA, THJ & PMM 1941: 148

Hedruris sp.

Crinia signifera, SA, AHC 28

Superfamily Filarioidea

Filarioidea ?gen. ?sp.

Filaria cochleata Railliet, 1916

syn. *Filaria spiralis* Oerley, 1882

Heleioporus albopunctatus, ?, Oerley 1882:
 312

Nematoda Not Further Identified

Agamonema sp.

Hyla caerulea, Qld, encysted larva, THJ 1914:
 82

Dorylaimid

Frog, SA, AHC 6417

Nematode larvae

Bufo marinus, Qld, cysts, Freeland et al. 1986:
 496

Hyla moorei, WA, BM(NH) 1980.298–307

Arenophryne rotunda, WA, cysts, AHC 6808

Hyla caerulea, Qld, cysts, AHC 2341

Nematodes

Bufo marinus, Qld, Freeland et al. 1986: 496,
 AHC 8,9, 2974, 3258

Crinia georgiana, WA, AHC 8081, 8079

Crinia glauerti, WA, AHC 8119, 8113

Crinia haswelli, Vic, AHC 8084

Crinia leai, WA, AHC 8115, 8082, 8078

Crinia pseudinsignifera, WA, AHC 8118, 8114

Crinia riparia, SA, AHC 8077

Crinia rosea, WA, AHC 8076

Crinia signifera, NSW, SJJ 1912:290; SA,
 AHC 20, 22–24, 3617, 6799, 8102, 8105; Vic,
 AHC 1083, 1098; NSW, AHC 8066

Crinia sp., Vic, AHC 21; SA, AHC 4210,
 4211, 4214, 4217, 4219, 4231–4233

Crinia subinsignifera, WA, AHC 8080, 8075

Crinia victoriana, Vic, AHC 8122, 8069,
 8070, 8088, 8096, 8099

Cyclorana australis, WA, AHC 12880

Heleioporus eryei, WA, AHC 8120

Hyla adelaidensis, NSW, AHC 1760

Hyla aurea, NSW, SJJ 1912: 291, AHC 3528,
 2306, 2308, 2309, 2314–2316, 2318–2321,
 2323, 2324; SA, AHC 3520

Hyla aurea raniformis, Vic, AHC 8094

Hyla caerulea, NSW, SJJ 1912: 290, AHC
 2339, 2337, 2336, 2333, 2360; NT, AHC 2331;
 Qld, AHC 2349, 2346, 2344, 2342, 2340,
 2338, 2335, 2235

Hyla dentata, NSW, SJJ 1912: 291

Hyla ewingii, NSW, SJJ 1912: 291; SA, AHC 8236
Hyla jervisiensis, SA, AHC 1759, 3615
Hyla lesueurii, NSW, SJJ 1912: 291; Qld, AHC 8238
Hyla peronii, NSW, SJJ 1912: 290; SA, AHC 12396
Hyla phyllochroa, NSW, SJJ 1912: 290
Kyarranus sphagnicolus, NSW, AHC 8247
Limnodynastes dorsalis, NSW, SJJ 1912: 290, AHC 2365, 3362, 2361, 2360; Vic, AHC 8068; Qld, AHC 2367; SA, AHC 2368, 3010, 3176, 8108, 8235
Limnodynastes fletcheri, NSW, AHC 8059
Limnodynastes peronii, NSW, SJJ 1912: 290, AHC 1728, 3477; SA, AHC 8103
Limnodynastes sp., Qld, AHC 2605
Limnodynastes tasmaniensis, NSW, SJJ 1912: 290, AHC 8064; Vic, AHC 36, 8087, 8100; SA, AHC 25, 26, 39, 1877, 1882, 3320, 3619, 3622, 5031, 8101, 8107, 8110, 12389
Litoria aurea, SA, AHC 8073
Litoria booroolongensis, NSW, AHC 8063
Litoria caerulea, Qld, AHC 8061, 8060
Litoria dahlui, NT, AHC 6809, 6993
Litoria ewingii, Vic, AHC 8071, 8072, 8095, 8097
Litoria nigrofrenata, Qld, AHC 6145
Litoria rothii, Qld, AHC 7181
Litoria verreauxii, NSW, AHC 8085
Mixophyes fasciolatus, Qld, AHC 8093, 8056
Neobatrachus pelobatoides, WA, AHC 8121, 8116
Neobatrachus pictus, SA, AHC 8104
Pseudophryne bibronii, Vic, AHC 8090; NSW, AHC 8062; SA, AHC 4213, 4218, 4220–4227, 8089, 8106, 8111
Pseudophryne guentheri, WA, AHC 8117, 8074
Pseudophryne occidentalis, WA, AHC 8112
Pseudophryne semimarmorata, SA, AHC 8109
Uperoleia marmorata, NSW, AHC 8055

3. Phylum Acanthocephala

Class Palaeacanthocephala Meyer, 1931
Order Echinorhynchida Southwell & MacFie, 1925

Family ECHINORHYNCHIDAE Cobbold, 1876

Acanthocephalus crinia Snow, 1971

Crinia tasmaniensis, Tas, Snow 1971: 147, TM K228–230, AHC 18165

Crinia laevis, Tas, Snow 1971: 147

Crinia signifera, Tas, Snow 1971: 147

Pseudoacanthocephalus perthensis Edmonds, 1971

Litoria moorei, WA, Edmonds 1971: 55; AHC

5048, 5051

Limnodynastes dorsalis, WA, Edmonds 1971: 55

Order Polymorphida

Family PLAGIORHYNCHIDAE Golvan, 1960

Porrorchis hylae (Johnston, 1914), Schmidt & Kuntz, 1967

syn. *Echinorhynchus* sp. Johnston, 1912;

Echinorhynchus hylae Johnston, 1914;

Echinorhynchus bulbocaudatus Southwell &

MacFie, 1925; *Gordiorhynchus hylae* (Johnston, 1914), Johnston & Edmonds, 1948;

Pseudoporrorchis hylae (Johnston, 1914), Edmonds, 1957

Limnodynastes dorsalis, SA, encysted larva, THJ & Edmonds 1948: 69

Bufo marinus, Qld, encysted larva, Freeland et al. 1986: 496 (identified by Edmonds 1989: 130)

Hyla aurea, NSW, encysted larva, THJ 1912: 84, THJ 1914: 83; SA, NSW, THJ & Edmonds 1948: 69

Hyla caerulea, Qld, encysted larva, THJ 1914: 83, THJ & Edmonds 1948: 69

Acanthocephala Not Further Identified

Acanthocephala sp.

Hyla caerulea, NSW, QM GL 12287

Hyla peronii, Qld, QM GL 12346

Acanthocephala

Limnodynastes sp., SA, AHC 3409; larva, AHC 3481

HOST - PARASITE CHECKLIST

Order Anura

Family MYOBATRACHIDAE

Adelotus brevis (Günther, 1863)

N *Rhabdias hylae*, (lung)

Arerophryne rotunda Tyler, 1976

N Nematode larva, cysts

Assa darlingtoni (Loveridge, 1933)

C *Cylindrotaenia minor*, (intestine)

Crinia georgiana Tschudi, 1838

N *Rhabdias hylae*, (lung)

N Nematodes, (duodenum, rectum)

Crinia glauerti Loveridge, 1933

N *Rhabdias hylae*, (lung)

N Nematodes, (buccal cavity, rectum, ileum)

Crinia haswelli Fletcher, 1894

see *Paracrinia haswelli*

Crinia insignifera* Moore, 1954**N *Rhabdias hylae*, (lung)Crinia laevis* Günther, 1864**see *Geocrinia laevis****Crinia leai* Fletcher, 1898**see *Geocrinia leai****Crinia parinsignifera* Main, 1957**C *Nematotaenia hylae*, (intestine)***Crinia pseudinsignifera* Main, 1957**

N Nematodes, (ileum)

***Crinia riparia* Littlejohn & Martin, 1965**C *Nematotaenia hylae*, (intestine)

N Nematodes, (rectum)

Crinia rosea* Harrison, 1927**see *Geocrinia rosea*Crinia signifera* (Girard, 1853)**

C proteocephalid plerocercoids, (mesentery & under skin)

C *Cylindrotaenia minor*, (duodenum, ileum)C *Nematotaenia hylae*, (duodenum)

C Cestodes, (small intestine)

N *Rhabdias hylae*, (lung)N *Hedruris* sp., (stomach)

N Nematodes, (stomach, intestine, buccal cavity, rectum, lung, abdominal cavity)

A *Acanthocephalus criniaie*, (duodenum, ileum)***Crinia signifera* (Girard, 1853) tadpole**D *Cercaria ellisi*, metacercaria, (kidney, mesenteries, heart lung), (experimental)***Crinia subinsignifera* Littlejohn, 1957**N *Rhabdias hylae*, (lung)

N Nematodes, (rectum)

Crinia tasmaniensis* (Günther, 1864)**C *Cylindrotaenia criniaie*, (duodenum, ileum)C *Cylindrotaenia minor*, (duodenum, ileum)A *Acanthocephalus criniaie*, (duodenum, ileum)Crinia victoriana* Boulenger, 1888**see *Geocrinia victoriana****Crinia* sp.**

C Cestodes, (intestine)

N Nematodes, (intestine, stomach, rectum)

***Geocrinia laevis* (Günther, 1864)**

C proteocephalid plerocercoids, (mesentery)

C *Cylindrotaenia minor*, (duodenum, ileum)A *Acanthocephalus criniaie*, (duodenum, ileum)***Geocrinia leai* (Fletcher, 1898)**N *Rhabdias hylae*, (lung)

N Nematodes, (abdominal cavity, duodenum)

***Geocrinia rosea* (Harrison, 1927)**

N Nematodes, (rectum)

***Geocrinia victoriana* (Boulenger, 1888)**N *Rhabdias hylae*, (lung)

N Nematodes, (duodenum, rectum)

Heleioporus albopunctatus* Gray, 1841**N *Parathelandros carinae*, (rectum)N *Filaria cochleata*, (encapsulated between serous and muscular layers of stomach)Heleioporus australiacus* (Shaw & Nodder, 1795)**N *Parathelandros carinae*, (rectum)N *Maxvachonia flindersi*, (rectum)***Heleioporus barycragus* Lee, 1967**N *Maxvachonia flindersi****Heleioporus eyrei* (Gray, 1845)**N *Parathelandros carinae*, (rectum)N *Parathelandros johnstoni*, (rectum)N *Austraplectana kartanum*, (rectum)N *Physaloptera* sp., (stomach)

Nematodes, (stomach)

Heleioporus inornatus* (Lee & Main, 1954)**N *Maxvachonia flindersi*, (rectum)Heleioporus psammophilus* (Lee & Main, 1954)**N *Parathelandros carinae*, (rectum)N *Maxvachonia flindersi*, (rectum)***Hyperolia marmorata* (Gray, 1841)**see *Uperoleia* spp.***Kyarranus loveridgei* (Parker, 1940)**C *Cylindrotaenia minor*, (intestine)***Kyarranus sphagnicolus* Moore, 1958**

N Nematodes, (rectum)

Leptodactylid* sp.**see *Myobatrachid* sp.Limnodynastes dorsalis* (Gray, 1841)**for *Limnodynastes dorsalis* from any state, except WA, see *Limnodynastes dumerilii*N *Parathelandros johnstoni*, (rectum)A *Pseudoacanthocephalus perthensis*, (intestine)***Limnodynastes dorsalis dumerilii***see *Limnodynastes dumerilii****Limnodynastes dumerilii* Peters, 1863**D *Gorgodera australiensis*D *Gorgodera* sp.D *Dolichosaccus ischyryus*, (intestine)D *Dolichosaccus trypherus*D *Dolichosaccus* sp.D *Dolichoperoides macalpini*, metacercaria, (tissues)

D Digenea cysts

D Digenea, (intestine, stomach)

N *Rhabdias hylae*, (lung)N *Oswaldocruzia limnodynastes*, (intestine)N *Parathelandros australiensis*, (rectum, intestine)N *Parathelandros limnodynastes*N *Parathelandros propinqua*, (rectum, intestine)

N Oxyurid

N *Cosmocerca limnodynastes*N *Maxvachonia flindersi*, (rectum)N *Physaloptera confusa*, encysted larva, (mesentery, stomach, peritoneum)N *Physloptera* sp., cysts

- N Nematodes, (stomach, intestine, rectum)
 A *Porrorchis hylae*, encysted larva, (mesenteries)
Limnodynastes fletcheri Boulenger, 1888
 D *Dolichosaccus* sp.
 D Digenea
 N *Rhabdias hylae*, (lung)
 N *Parathelandros australiensis*, (rectum)
 N Nematodes, (duodenum, rectum)
Limnodynastes ornatus (Gray, 1842)
 C *Nematotaenia hylae*, (intestine)
Limnodynastes peronii (Duméril & Bibron, 1841)
 D *Diplodiscus megalochrus*, (rectum)
 D *Gorgodera australiensis*, (bladder)
 D *Dolichosaccus anartius*, (intestine, rectum)
 D *Dolichosaccus trypherus*, (duodenum)
 D *Haematoleochus australis*, (lungs)
 C proteocephalid plerocercoids, (mesentery)
 N *Rhabdias hylae*, (lungs)
 N Nematodes, (lungs, intestine, rectum, stomach)
Limnodynastes tasmaniensis Günther, 1858
 D *Diplodiscus microchrus*, (rectum)
 D *Gorgodera* sp.
 D *Dolichosaccus trypherus*, (intestine)
 D *Dolichosaccus* sp.
 D *Dolichoperoides macalpini*, metacercaria (tissues)
 D Diplostomula, (buccal cavity)
 D Strigeid, cysts
 D Digenea cysts, (muscles, subcutaneous)
 D Digenea, (gut)
 N *Rhabdias hylae*, (lung)
 N Oxyurids, (abdominal cavity)
 N *Physaloptera confusa*, encysted larva, (stomach, peritoneum)
 N Nematodes, (lungs, stomach, intestine, rectum)
Limnodynastes tasmaniensis Günther, 1858 tadpole
 D *Cercaria angelae*, cysts, (wall of thorax and rectum, pericardium, tail tissue, base of foreleg), (experimental)
 D *Cercaria natans*, (kidney tissue, kidney peritoneum), (experimental)
Limnodynastes tasmaniensis (platycephalus) Günther, 1867
 see *Limnodynastes tasmaniensis*
***Limnodynastes* sp.**
 D Diplostomula, (eye), (experimental)
 D Digenea, (stomach, intestine, rectum)
 C Cestodes, (coelom)
 N Nematodes, (stomach)
 A Acanthocephala, (mesentery)
 A Acanthocephala, larva, (rectum)
***Limnodynastes* sp. tadpole**
 D *Cercaria amerianna*, diplostomula, (tissues), (experimental)
 D *Dolichoperoides macalpini*, metacercaria, (tissues)
Metacrinia nichollsi (Harrison, 1927)
 C Cestodes
Mixophyes fasciolatus Günther, 1864
 N *Rhabdias hylae*, (lung)
 N Nematodes, (rectum)
Mixophyes fasciolatus Günther, 1864 tadpole
 D *Fibricola intermedius*, metacercaria, (muscles)
***Mixophyes* sp.**
 N Oxyurid
***Myobatrachid* sp.**
 D *Fibricola intermedius*, metacercaria, (muscle)
Neobatrachus centralis (Parker, 1940)
 N *Parathelandros johnstoni*, (rectum)
Neobatrachus pelobatoides (Werner, 1914)
 N *Parathelandros carinae*, (rectum)
 N *Parathelandros johnstoni*, (rectum)
 N Nematodes, (rectum)
Neobatrachus pictus Peters, 1863
 N Nematodes, (rectum)
Paracrinia haswelli (Fletcher, 1894)
 N Nematodes, (duodenum, rectum)
Philoria loveridgei Parker, 1940
 see *Kyarranus loveridgei*
Pseudophryne bibronii Günther, 1858
 N *Rhabdias hylae*, (lung)
 N Nematodes, (duodenum, rectum, stomach)
Pseudophryne guentheri Boulenger, 1964
 N *Rhabdias hylae*, (lung)
 N Nematodes, (rectum)
Pseudophryne occidentalis Parker, 1940
 N *Rhabdias hylae*, (lung)
 N Nematodes, (rectum, stomach)
Pseudophryne semimarmorata Lucas, 1892
 N Nematodes, (rectum)
***Pseudophryne* sp.**
 N *Rhabdias hylae*, (lung)
***Ranidella* spp.**
 for all *Ranidella* species, see the *Crinia* equivalent
Rheobatrachus silus Liem, 1973
 D Digenea, (rectum)
 C Cestodes
Taudactylus diurnus Straughan & Lee, 1966
 D Digenea, (rectum)
Uperoleia marmorata Gray, 1841
 for *Uperoleia marmorata* from all states, except WA, see *Uperoleia* spp.
Uperoleia rugosa (Andersson, 1916)
 C *Nematotaenia hylae*, (intestine)
***Uperoleia* spp.**
 C *Nematotaenia* sp.
 C Cestodes, (small intestine)
 N Nematodes, (rectum)

Family HYLIDAE

Chiroleptes brevipalmatus Peters, 1871see *Cyclorana brevipes****Cyclorana australis*** (Gray, 1842)N *Physaloptera* sp., larva, (buccal cavity)

N Nematodes

Cyclorana brevipes (Peters, 1871)D *Dolichosaccus juvenilis*, (intestine)***Cyclorana cultripipes*** Parker, 1940

D Allocreadiidae sp.

D *Dolichosaccus juvenilis*D *Mesocoelium microon****Cyclorana novaehollandiae*** Steindachner, 1867N *Nematotaenia hylae*, (intestine)***Cyclorana* sp.**

N Oxyurids, (rectum)

Hyla* spp.**for all *Hyla* species, see the *Litoria* equivalent, with the following exceptions:i) *Hyla aurea* Lesson, 1829for *Hyla aurea* from NSW (coastal area), see *Litoria aurea*for *Hyla aurea* from SA, Tas, Vic, NSW (exclusive of coastal area), see *Litoria raniformis*for *Hyla aurea* from WA, see *Litoria* spp.ii) *Hyla ewingi alpina* Fry, 1915see *Litoria verreauxii*iii) *Hyla jervisiensis* Duméril & Bibron, 1841for *Hyla jervisiensis* from all states, except SA, see *Litoria jervisiensis*for *Hyla jervisiensis* from SA see *Litoria ewingii*Litoria adelaidensis*** (Gray, 1841)for *Litoria adelaidensis* from all states, except WA, see *Litoria* spp.N *Parathelandros maini*, (rectum)N *Maxvachonia flindersi*, (intestine)***Litoria aurea*** (Lesson, 1829)for *Litoria aurea* from Vic, Tas, SA, NSW(exclusive of coastal area), see *Litoria raniformis*for *Litoria aurea* from WA, see *Litoria* spp.D *Diplodiscus megalochrus*, (rectum)D *Diplodiscus* sp., (rectum)D *Distoma* sp.D *Gorgodera australiensis*, (bladder)D *Gorgodera* sp., (bladder)D *Haematoleochus australis*, (lungs)D *Dolichosaccus anartius*, (intestine, rectum)D *Dolichosaccus trypherus*, (duodenum)D *Dolichosaccus* sp.D *Mesocoelium mesembrinum*D *Pleurogenoides solus*, (intestine)

D Digenea cysts, (nerves, muscles, subcutaneous)

D Digenea, (lung, intestine, rectum)

C ?*Ligula* sp., (muscles, peritoneal cavity, subdermal lymph sinuses)

C Diphyllbothriidae spargana, (thigh muscles)

C *Ophiotaenia* sp., (intestine)C *Proteocephalus hylae*C *Triplotaenia mirabilis*

C Cestodes, (intestine, muscle)

N *Rhabdias hylae*, (lung)N *Rhabdias nigrovenosum*, (lung)N *Rhabdias* sp., (lung)N *Rhabdonema* sp.N *Oswaldocruzia limnodynastes*, (intestine)N *Falcaustra hylae*, (intestine)N *Physaloptera confusa*, encysted larva, (mesentery)

N Nematodes, (lung, intestine, rectum, peritoneum, abdominal cavity, stomach)

A *Porrorchis hylae*, encysted larva, (mesenteries)***Litoria booroolongensis*** (Moore, 1961)

N Nematodes, (rectum, mesentery)

Litoria caerulea (White, 1790)D *Diplodiscus megalochrus*D *Diplodiscus* sp.D *Dolichosaccus ischyryus*, (intestine)D *Dolichosaccus symmetrus*, (rectum)D *Dolichosaccus* sp.D *Mesocoelium megaloon*, (intestine)D *Mesocoelium mesembrinum*, (intestine, duodenum)D *Mesocoelium microon*D *Mesocoelium* sp.D *Fibricola intermedius*, metacercaria, (muscles) paratenic hostD *Halipegus* sp.

D Digenea, (intestine)

C ?*Ligula* sp.

C Diphyllbothriidae spargana, (thigh muscle)

C *Nematotaenia* sp.

C Cestodes, (rectum)

N *Rhabdias hylae*, (lung)N *Rhabdonema* sp., (lungs)N *Parathelandros mastigurus*, (small intestine, rectum)

N Oxyurid, (intestine)

N *Maxvachonia flindersi*N *Physaloptera confusa*, encysted larva, (stomach, peritoneum)N *Agamonema* sp., encysted larva, (stomach wall)

N Nematode larva, cysts, (intestine)

N Nematodes, (stomach, intestine, rectum, lung, buccal cavity, abdominal cavity, muscle)

A *Porrorchis hylae*, encysted larva, (liver)A *Acanthocephala* sp.***Litoria citropa*** (Duméril & Bibron, 1841)M *Parapolytoma bulliense*D *Mesocoelium oligoon*, (duodenum)***Litoria cyclorhyncha*** (Boulenger, 1882)

- N *Parathelandros maini*, (rectum)
 N *Maxvachonia flindersi*, (rectum)
Litoria dahlui (Boulenger, 1896)
 D Digenea
 N Nematodes
Litoria dentata (Keferstein, 1868)
 N Nematodes, (intestine)
Litoria ewingii (Duméril & Bibron, 1841)
 D *Diplodiscus microchrus*, (rectum)
 D *Mesocoelium megaloon*, (intestine)
 C *Nematotaenia hylae*, (duodenum)
 C Cestodes, (small intestine)
 N *Austraplectana kartanum*
 N *Maxvachonia flindersi*
 N *Hedruris hylae*
 N Nematodes, (intestine, rectum, duodenum, mesentery)
Litoria fallax (Peters, 1880)
 C *Nematotaenia hylae*, (intestine)
Litoria freycineti Tschudi, 1838
 D *Dolichosaccus diamesus*, (stomach)
 D *Pleurogenoides freycineti*, (duodenum)
 C *Nematotaenia* sp.
 C Cestodes, (duodenum)
Litoria gracilentia (Peters, 1869)
 D *Mesocoelium microon*
 N *Parathelandros mastigurus*, (rectum)
Litoria inermis (Peters, 1867)
 C *Nematotaenia hylae*, (intestine)
 N *Pseudorictularia disparilis*, (stomach)
Litoria infrafronata (Günther, 1867)
 N *Maxvachonia adamsoni*, (intestine)
Litoria latopalmata Günther, 1867
 C Diphyllbothriidae spargana, (muscles), (experimental)
 C *Nematotaenia hylae*, (intestine)
 N *Rhabdias hylae*, (lung)
Litoria latopalmata Günther, 1867 tadpole
 D *Fibricola intermedius*, metacercaria, (muscles)
 C Diphyllbothriidae spargana, (experimental)
Litoria lesueurii (Duméril & Bibron, 1841)
 M *Parapolyistoma bulliense*, (bladder)
 N *Rhabdias hylae*, (lung)
 Nematodes, (rectum)
Litoria moorei (Copland, 1957)
 D *Haematoleochus australis*, (lungs)
 D *Dolichosaccus tryphurus*, (intestine)
 D Digenea, (abdominal cavity)
 C *Proteocephalus hylae*, (intestine)
 N *Rhabdias* sp.
 N *Parathelandros maini*, (rectum)
 N *Austraplectana kartanum*, (rectum)
 N *Maxvachonia flindersi*, (rectum)
 N Nematode larvae
 A *Pseudoacanthocephalus perthensis*, (rectum, intestine)
Litoria nasuta (Gray, 1842)
 N *Austraplectana kartanum*
 N *Maxvachonia ewersi*
Litoria nigrofrenata (Günther, 1867)
 N *Pseudorictularia disparilis*, (stomach)
 N Nematodes
Litoria nyakalensis Liem, 1974
 M *Parapolyistoma* sp., (urinary bladder)
Litoria pallida Davies, Martin & Watson, 1983
 C *Nematotaenia hylae*, (intestine)
Litoria pearsoniana Copland, 1961
 M *Parapolyistoma bulliense*, (bladder)
 D *Fibricola intermedius*, metacercaria, (muscles) (natural & experimental)
Litoria peronii (Tschudi, 1838)
 D Diplostomula
 D Digenea cysts, (rectum)
 D Digenea
 C *Nematotaenia hylae*, (intestine)
 N *Rhabdias hylae*, (lung)
 N *Oswaldocruzia limnodynastes*
 N *Physaloptera confusa*, encysted larva, (mesentery)
 N Nematodes, (lungs, rectum)
 A *Acanthocephala* sp.
Litoria phyllochroa (Günther, 1863)
 M *Parapolyistoma bulliense*, (bladder)
 N Nematodes, (rectum)
Litoria raniformis (Keferstein, 1867)
 D *Gorgodera* sp., (bladder)
 D *Haematoleochus australis*
 D *Dolichosaccus tryphurus*, (intestine)
 D *Dolichoperoides macalpini*, metacercaria, (intestine)
 D Diplostomula
 D Echinostome cysts, (stomach)
 D Plagiorchid cysts
 D Strigeid cysts, (body wall)
 D *Tetracotyle* cysts
 D Digenea, (intestine)
 C *Ophiotaenia* sp., (intestine)
 C proteocephalid plerocercoids
 C Cestodes
 C Cestode larva, (abdominal cavity)
 N *Rhabdias hylae*, (lung)
 N *Rhabdias* sp., (lung)
 N *Rhabdonema* sp.
 N *Oswaldocruzia limnodynastes*, (intestine)
 N Oxyurids, (lung, rectum)
 N *Physaloptera* sp.
 N Nematodes, (mesentery, intestine, stomach, rectum)
 A *Porrorchis hylae*, encysted larva, (mesentery)
Litoria rothii (De Vis, 1884)
 D Digenea, (small intestine)

N Oxyurid
N Nematodes, (small intestine)

Litoria rubella (Gray, 1842)

C *Spirometra erinacei*
N *Parathelandros* spp., (rectum)
N Oxyurid

Litoria verreauxii (Duméril, 1853)

C Cestodes, (small intestine)
N Nematodes, (rectum)

***Litoria* spp.**

D *Dolichosaccus* spp.
D *Pleurogenes* spp.
C Cestodes

***Litoria* spp.**

identified as *Litoria adelaidensis* from NSW
N Nematodes

***Litoria* spp.**

identified as *Litoria aurea* from WA
C Diphyllbothriidae spargana, (thigh muscle)
N *Parathelandros* spp.

Family RANIDAE

Rana daemeli (Steindachner, 1868)

N *Rhabdias australiensis*, (lung)
N Cosmocercinae gen. sp. 1
N *Seuratscaris numidica*, (stomach, intestine)
N *Pseudorictularia disparilis*

Family BUFONIDAE

Bufo marinus (Linnaeus, 1758)

D *Diplodiscus* sp.
D Amphistome
D *Dolichosaccus symmetricus*, (intestine)
D *Dolichosaccus* sp.
D *Mesocoelium mesembrinum*, (small intestine)
D *Mesocoelium* sp., (intestine, abdominal cavity)
D Lecithodendriid sp., (intestine)
D *Zeylanurotrema spearei*, (urinary bladder)
D Digenea cysts
D Digenea, (intestine, stomach, rectum, abdominal cavity, lung, buccal cavity)
C Diphyllbothriidae spargana
C ?*Spirometra mansonii*, spargana, (muscles)
C Proteocephalid plerocercoids
C *Nematotaenia hylae*, (intestine)

C Cestodes, (intestine, stomach)
N *Parathelandros mastigurus*
N *Parathelandros* spp., (intestine)
N Oxyurid
N *Maxvachonia flindersi*, (rectum)
N Cosmocercoid
N Nematode cysts
N Nematodes, (intestine, rectum, abdominal cavity, stomach wall)
A *Pororchis hylae*, encysted larva

Unidentified Anura

Frog

D *Diplodiscus megalochrus*, (bladder)
D Echinostome cysts, (stomach)
D Digenea cysts
C Cestodes, (buccal cavity)
N *Austraplectana* sp.
N *Ophidascaris pyrrhus*
N Dorylaimid, (intestine)

Tadpole

D *Dolichoperoides macalpini*, metacercaria
D *Cercaria ameriannae*, diplostoma
D *Cercaria angelae*, cysts, metacercaria
D *Cercaria ellisi*, cysts
D *Cercaria lethargica*
D K.I. Stylet cercaria, (experimental)
D J.W. Stylet metacercaria
D Echinostome J cercaria, (experimental)
D Echinostome cysts, (experimental)
D Digenea cysts
D Digenea cysts, (experimental)
N *Ophidascaris pyrrhus*, (experimental)
N *Rallietascaris varani*

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MATERIAL CULTURE TRADITIONS OF THE WIK PEOPLE, CAPE YORK PENINSULA

P. SUTTON

Summary

This paper draws upon the author's fieldwork among the Wik people since the 1970s to present a summary of the material culture traditions of central-western Cape York Peninsula. Historical sources, particularly the ethnographics of the anthropologists Ursula McConnel and Donald Thomson, provide additional detail.

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P. SUTTON

SUTTON, P. 1994. Material culture traditions of the Wik people, Cape York Peninsula. *Rec. S. Aust. Mus.* 27(1): 31–52.

This paper draws upon the author's fieldwork among the Wik people since the 1970s to present a summary of the material culture traditions of central-western Cape York Peninsula. Historical sources, particularly the ethnographies of the anthropologists Ursula McConnel and Donald Thomson, provide additional detail.

P. Sutton, 7 Edgeware Road, Aldgate, South Australia, 5154. Manuscript received 4 April, 1993.

Since the 1970s the Australian Aboriginal people whose traditions of material culture are presented here have been known to anthropologists as 'the Wik speaking peoples' or just simply 'the Wik', but there is no cover term for them in their own languages, nor is there any evidence of such a term in the past. They share most of their autogenous material culture with their near neighbours, but in several ways they remain a recognisable cultural entity. Their focal area lies between the Archer and Edward Rivers, western Cape York Peninsula, Queensland, and inland to Coen. Most Wik people still live in this triangle (Fig. 1).

The Wik include most of the population of Aurukun and its outstations (hence 'Aurukun people') and that part of Pormpurraaw's population known as 'Mungkan side'. They also include west-side people affiliated with languages such as Mungkanho and Wik-Iiyeyn who live at Coen and Meripah in central Cape York Peninsula. The Wik-Way, with countries between Aurukun and the Mission River to the north, are now also effectively Wik people through culture change in the present century. Misleading cover-terms for the Wik include 'the Wik-Mungkan' and 'the Aurukuns', the latter sometimes occurring in news media.

The people discussed in this paper are those who are members of clans with traditional estates along the coast south from Love River to between Christmas Creek and Breakfast Creek, and inland from the middle Archer River south via Rokeby and Meripah to the upper Holroyd. There are perhaps fifty such estates clustered intensively along the narrow coastal flood-plain and occupying very much larger expanses in the forest and savannah woodland country of the uplands. Detailed maps and site records for many of these estates are to be found in Sutton, Martin, von Sturmer, Cribb & Chase (1990). For detailed studies of the traditional land relationship systems in the area see especially Sutton (1978) and von Sturmer (1978).

The most dramatic environmental feature of the region is the contrast between the food- and resource-rich coastal strip, at times only a few kilometres wide and subject to massive wet season flooding, and the vast, gently undulating hinterland with its relatively simple flora and restricted faunal range broken only here and there by riverine gallery forest and its complex of resources.

Proceeding inland from the coast, the major environmental zones are:

1. the beach dunes, grading from fine sand to coarse shellgrit, sparsely shaded and offering limited saltwater resources in the intertidal zone;
2. the dune woodland along the eastern edge of zone 1; extremely rich and complex both florally and faunally;
3. grassy flood plains and huge saltpan/mangrove areas, rich in birdlife and, in its freshwater lakes or in its tidal estuaries and waterholes, rich in marine life; inundated during and after the wet season;
4. another zone of dune woodland on Pleistocene sandridges, running approximately in parallel with the present coast; rich and complex in patches;
5. relatively open bloodwood and eucalypt forest, punctuated by intermittent, broad watercourses bearing melaleucas, and containing a large number of permanent swamps;
6. riverine gallery forest fringing permanent streams characterised by white sandy beds in many sections (chiefly the Archer River system; also Kendall River);
7. grassy savannah woodland with occasional outcrops of stone and gravel; this is generally the westernmost limit of European pastoral activity, although the Aboriginal communities have turned off cattle from the coastal area at various times since the 1930s.

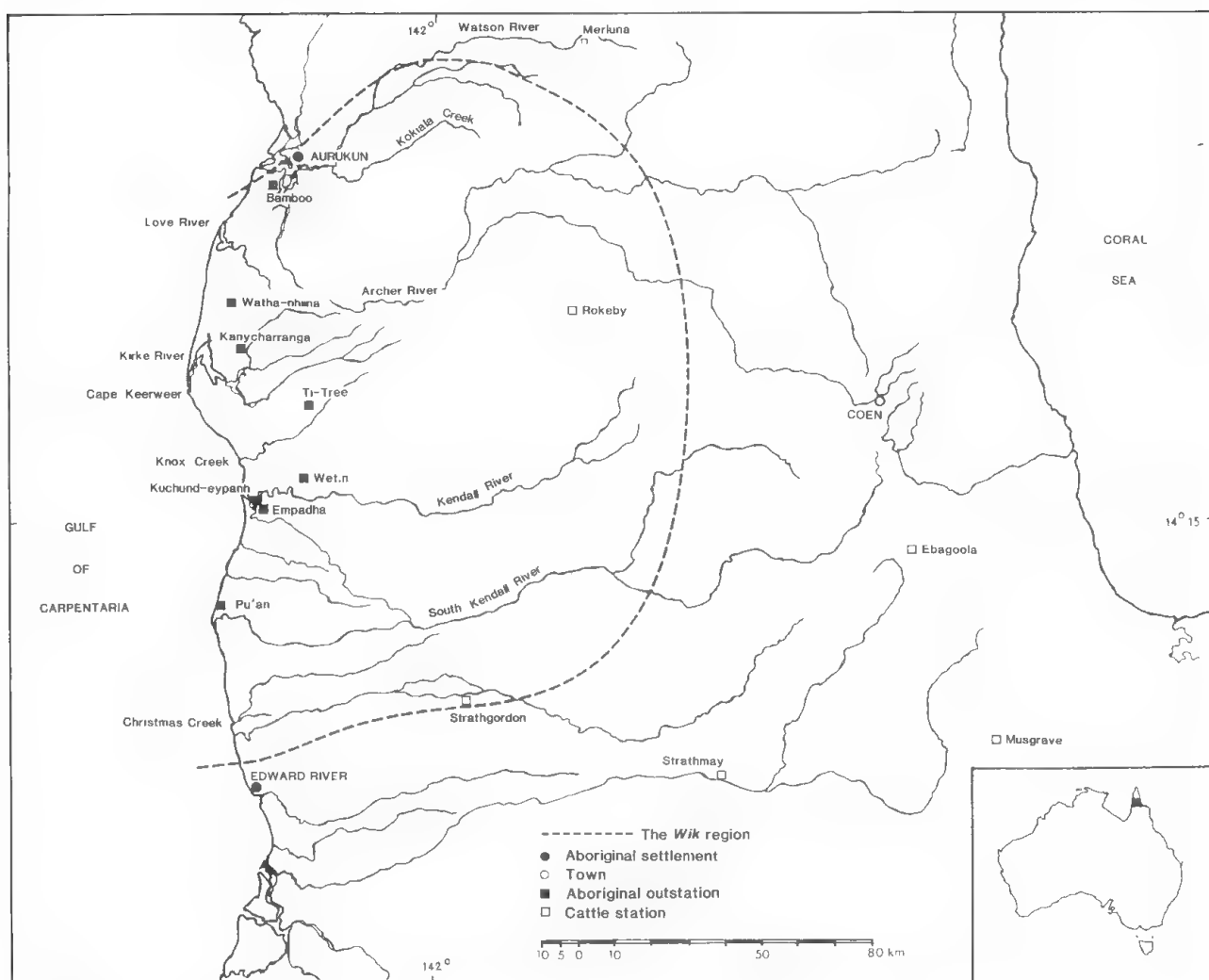


FIGURE 1. The Wik region.

SOCIO-CULTURAL GROUPS

The most important social distinction within the Aboriginal population of the region is that between 'top side' and 'bottom side', a reflection of the origins of most of the Wik in countries located either inland ('top side') or on the coastal strip ('bottom side'). Traditions of material culture also reflect this distinction, which is one that has been under-recognised by some previous anthropological writers (e.g. Thomson 1939a, McConnel 1953).

Among the coastal peoples it is possible to recognise major subgroups consisting of those whose clan estates cluster around certain rivers or creeks. Thus there are, going from north to south, the Love River people, those of the Kirke River ('Cape Keerweer people'), Knox River people, Kendall River people and so on. These are not linguistic groups, but regional groups which have tended to closely intermarry, share religious cults, and unite at times in conflict with others. In the 1980s and 1990s the clarity and prominence of these distinctions were waning while the top/bottom

distinction was being strongly maintained. At the same time, the old regional ceremonial divisions (Apalach, Puch, Wanam etc.) were still known but their ceremonies were being performed less often, less fully, and in fewer contexts.

There are no simple political linguistic groups ('dialectal tribes') in this region (see Sutton 1978, Rigsby & Sutton 1980-82). The people do own, by right of clan birth and country, a recognised variety of languages. In the case of the Wik, all of these languages belong to a single genetic family known as the Wik group. About fifteen named languages constitute this group. This includes languages named with the prefix 'Wik-' ['Language-'] (for example: Wik-Mungkan, Wik-liyanh, Wik-Ngathan, Wik-Ngatharr, Wik-Ep, Wik-Me'anh, Wik-Keyangan), those named with the prefix 'Kugu-' ['Language-'] (for example: Kugu-Uwanh, Kugu-Muminh, Kugu-Ugbanh, Kugu-Mu'inh), and some with no prefix (e.g. Mungkanho).

Adults and most children have variable knowledge of many of these languages, including full competence in up to four or five in some cases,

although several of these languages were in advanced stages of decline and some were virtually extinct by the late 1970s (Sutton 1978). By the 1980s and 1990s Wik-Mungkan and English were the dominant languages of the Aurukun area, and Wik-Mungkan was the first language of most children. Several hundred people, however, had partial or excellent knowledge of Wik-Ngathan or Wik-Ngatharr, and most languages had at least some surviving speakers.

Prehistory

The archaeology of the region was virtually unknown as late as 1985. Roger Cribb has carried out some preliminary survey work (Cribb 1986, Cribb *et al* 1988), paying particular attention to the spectacular shell mounds mapped at Love River by Cribb, Sutton, Martin and Chase in 1985. The Aboriginal custodians of these mound sites, as well as their neighbours, consider the mounds to be of non-human origin and to be 'story places'.

Perhaps the most interesting fact about the prehistory of the area is that the zone of greatest recent population, the coastal plains and dune systems, is geologically very young. The coast has been prograding, probably under constant human occupation, for about 6 000 years (Rhodes 1980). The human role in its formation as a mosaic of vegetational complexes has yet to be investigated in any detail.

Population

In 1988 some 900 Wik people lived at Aurukun and its handful of outstations. A few hundred more lived at Edward River, Coen, Kowanyama, Mornington Island and other centres such as Cairns. Their numbers had been increasing for some decades, after an initial sharp drop caused by European, Asian and Islander (Torres Strait and Pacific) incursions into the wider region in the late nineteenth and early twentieth centuries.

In 1930 Ursula McConnel estimated the coastal Wik people to number two or three hundred (1930: 99). She thought that 'the Wik-Mungkan' had originally numbered 1 500–2 000 people before the inroads of exotic diseases (1930: 181). In 1965 the Aurukun Aboriginal population, which contained most of the Wik people then alive, was 603 (Long 1970). Only sixteen years earlier the majority of the Wik population had been classed as 'nomads', living in the reserve but in touch with the mission since at least 1938. By 1957, most of the Kendall and Holroyd Rivers people had settled at Edward River or Aurukun, leaving only a small group (Tiger's mob) still living in the bush by the

1970s (Long 1970: 144–5; J. von Sturmer pers comm).

In pre-mission times population density along the coastal plains and dune systems was an estimated one person to 2.3 square miles (5.91 square kilometres; Sutton 1978: 90). This figure is based on a reconstruction using clan maps and an estimate of an average 20 persons per clan. A little further to the south, in the Mitchell River region, Sharp came to a comparable figure of one person to 2.4 square miles (6.19 square kilometres) in a census of bush-dwelling coastal people in 1932 (Sharp 1940: 487). These figures are at the high-density end of the scale for Australian Aborigines (see Maddock 1972: 22–3) and are vastly higher than what one might expect for the hinterland groups, where parallel figures available.

MATERIAL CULTURE

Raw materials

The coastal Wik region is practically devoid of stone and certainly devoid of hard stone suitable for tool-making. There are stony ridges, however, in the hinterland far to the east. In many months of combing the coastal and peri-coastal country while mapping old habitation and other sites with Wik people this author has only found two stone artefacts, both axe heads. Such stone must have been traded in from a long distance. Apart from local ochres, and the mud and shale used in cooking, most raw materials come from plants (wood, bark, seedpods, grass stems, leaves, sap) and animals (bone, teeth, feathers, shell, spines, wax, hair).

Settlement and shelter

In recent decades most Wik people have made use of tropical western-style housing when living in a settlement village such as that of Aurukun (Fig. 2). On the fringes of settlements and at outstations and temporary bush camps they make use of tin sheds, corrugated iron lean-tos, and tents. Leafy branches are used for daytime shades and when not using a house people would sleep in the open on the ground or, in earlier days, on elevated platforms during the dry months of the year. Houses and sheds were used to store possessions and to keep food from the unwanted reach of dogs and visitors, and were often too hot to use in the daytime. People tended to live under and near, rather than in, a modern house, up to the 1980s.

Thomson (1939a: 218) illustrated and described the traditional camps and house types of the region. Wet season huts on the coast (Fig. 3) were made of



FIGURE 2 Modern housing with group preparing for ceremonial house-opening, Aurukun 1987 Photo: Dale Chesson

melaleuca bark (especially *M. leucadendron* (L.) L. and *M. viridiflora*). In the inland areas the huts were of stringybark (*Eucalyptus tetradonta* Thomson 1939a: 218) or messmate (*Garcenia warrenii* F. Muell. Sutton & Smyth 1980 item 60). These two types of hut were given distinct names in languages such as Wik-Ngathan and Wik-Mungkan and were among the many typifiers of differences between the salt-water people and their inland neighbours, the fresh-water people. Melaleuca bark is the preferred material.

On the coast, wet season camps were generally located under the huge spreading branches of trees such as the fig (*Ficus microcarpa* L.f.) or the milkwood (*Alstonia actinophylla* (A. Cunn.) K. Schum.), where the circular depressions of the floors of earlier huts could still be seen in the dune sands in the 1980s. These trees were a protection against torrential rain and stormy winds. The huts were filled with smoke from a small internal fire and their one or two small entrances closed off once people were inside, to keep mosquitoes at bay. Dry



FIGURE 3. Wet-season hut of melaleuca bark, Archer River, 1930s. Photo: U. McConnel

season day camps also favoured large shade trees, and therefore dune woodland or upland forest environments, and were often at some distance from night camps. A quickly erected day shade was made by cutting young saplings and leaning them like a brush fence against a pole or spear resting on forks of two adjacent trees. A siesta under shade in the heat of the day was common practice, especially for older people who had spent the small hours of the morning awake, tending fires and keeping watch.

Night bush camps in dry weather were generally in entirely open environments such as level parts of sand dunes, salt-pans, coastal swales or grass plain. The preferred dry season camp was soft sand, free of grass or trees, offering long-distance all-round visibility as a defence against snakes and human intruders, and catching a breeze which would keep the mosquitoes down (see Thomson 1939a Plate 23).

Fire

Before matches were introduced, and in remote bush camps of the 1970s when matches had run out, a fire-drill was used (Fig. 4). Two lengths of young wood from the firestick tree (*Premna* sp.) of 100 to 150 centimetres were stripped and dried and carried



FIGURE 4. Fire-making, Cape York Peninsula 1930s. Photo: U. McConnel.

in a distinctive bamboo socket bound by yellow orchid stem and decorated with jequirity ('crab's eyes' or 'gidigidi') beads (*Abrus precatorius* L.). One of the sticks was held on the ground by the foot while the other was twirled by a person who stood up during the process. While *Premna* sp. was the preferred firestick wood, young stalks of the spear-handle tree *Hibiscus tiliaceus* L. were also used.

During field work in 1979, Dermot Smyth and this author recorded 37 botanically distinct types of firewood in the coastal and near inland zones between Archer River and Holroyd River. Our informants included older people who had lived their early lives in the bush, away from the mission. Of the various firewoods, 15 were considered good to excellent, 19 were considered acceptable, one was of use only as a last resort, one was regarded as tinder for lighting a fire, and another was only mentioned as kindling wood (any dry grass or fine dry twigs could be used as kindling). The preferred firewoods are marked as such in Sutton & Smyth 1980.

Fire was a constant factor in camp life, in travel, and in the hunting economy. Decisions on where to place hearths, how many hearths were required for a camp, how individuals oriented their heads when sleeping next to fires, and from whose fire a brand could be taken for the starting of another fire, all had important implications for the definition and negotiation of relationships between individuals and groups. In all the Wik languages, 'wife' is 'woman fire(-from)' and 'husband' is 'man fire(-from)'. The significance of fire and its sharing in traditional Western Cape York Peninsula culture is described in some detail by Thomson (1932).

In the course of a day, a particular individual might sit at several different fires within the same camp. In the daytime, a young bachelor might use a fire lit for a brief amount of cooking or boiling a billy for tea on a hot exposed patch of sand near a day-shade but in the full sun. Back at the base camp, in the evening, he might sit and eat with his parents or his sister and brother-in-law. For sleep, though, he might go to a fire which formed the nucleus of a sleeping-place for several other unattached adult men.

When people were dependent entirely on hunting and gathering for food, sections of grass-plain were fired systematically in the coastal region so that small mammals and reptiles could be harvested. As the vegetation dried off after the wet season, people set fire to the bush wherever they went, in order to clear the country for better hunting, for protection from snakes, for ease of travel and for improved visibility in the constant watch for enemies. These fires also marked the positions of bands of people, providing important information to their neighbours about their direction of travel. In the 1990s it was



FIGURE 4. Women digging water lilies, Archer River, 1930s. Photo: U. McConnel.



FIGURE 6. Women gathering water-lily seeds and pods, Archer River, 1930s. Photo: U. McConnel.

still normal practice to fire country during bush trips by vehicle and to light small fires as a signal of one's approach to an outstation camp. Rights in the firing of one's clan estate were not open to all, however, and disputes could arise over wrongful firings.

Subsistence activities

The basic facts of the seasonal regime and traditional subsistence economy in the region are well known, and have been the subject of publications by Thomson (1939a), McConnel (1953, 1957), and Chase and Sutton (1981). (See also von Sturmer 1978.) The following summary emphasises material culture and also contains new information.

The major vegetable foods in the pre-settlement economy were tubers, waterlilies, and an enormous variety of fruits. Nuts, the soft inner bark of two fig species, and the core of a *Livistona* palm were also eaten. Digging sticks were used, mainly by women, to obtain arrowroot (*Tacca leontopetaloides* (L.) Kuntze), round yams (*Dioscorea sativa* var. *rotunda*) and long yams (*Dioscorea transversa* R. Br.), which constituted staples (Fig. 5). Other tubers

such as the *Cayratia* spp. known as *kaayketh* and *walken* respectively (in Wik-Ngathan) were cooked in the ashes (along the coast), or in an earth oven (inland), but were not major foods. Of the tubers, only long yams were still commonly dug in the 1980s, as their preparation (brushing the sand off) and cooking (in ashes) required little effort.

Another staple was the lotus lily (*Nymphaea lotus* L. var. *australis* F. M. Bailey). Its young stems were eaten raw and its roots and seeds roasted. Even the flowers yielded sweet morsels. It was extremely abundant in the wetlands of the coastal region (Fig. 6).

Like the arrowroot and round yam, mangrove fruits provided abundant foods but also required considerable processing. In particular, the grey mangrove (*Avicennia marina* (Forssk. Vierh.)) and the small black mangrove (*Bruguiera gymnorhiza* (L. Lam.)) provided bulk carbohydrate, although by the 1970s these foods were no longer in any regular use.

The sweeter fruits, mainly growing on jungle trees in the dune woodland zones, were usually eaten raw, although several species were cooked because of their tartness when raw. Sutton and Smyth list seventeen fruits of these kinds (1980).



FIGURE 7. Women using baler shell to obtain water from a well to wash, Archer River, 1930s. Photo: U. McConnel.



FIGURE 8. Spearing fish with a two-pronged spear and spearthrower, Archer River, 1930s. Photo: U. McConnel.

The major ones were the yellowfruit or nonda apple (*Parinari nonda* F. Muell. ex. Benth.) which was collected in large quantities and stored; the various *Eugenia* and *Ficus* species (several of each); the black cherry (*Mallotuspolyadenus* F. Muell.); the redfruit (*Mimusops elengi* L.); the wild mango (*Planchonia careya* (F. Muell.) Knuth.); the wongai or black cherry (*Pouteria sericea* (Aiton) Baehni); and some of the *Terminalia* spp..

One of the figs, the pandanus and the 'monkey nut' tree (*Sterculia quadrifida* R. Br.) provided nuts which required different levels of preparation for eating.

Wild honey from the various *Trigona* spp. was a much sought-after food, occurring in relative abundance in the woodland region east of the flood plain and on some sandridges in the coastal zone. Stone axes (see McConnel 1953: Plate 12; b & p.24) were important for obtaining bee nests from hollow trees, but axe heads were traded in from elsewhere (McConnel 1953: 11). During the 1970s this author found a ground axehead at Uthuk Awuny (Big Lake) but it appeared to have had its blade abraded through use as a pounder. Hafted stone pounders are

reported from the area nearby to the south (Thomson 1936: Plate 8).

Mice, bandicoots and reptiles such as lizards and edible snakes were dug from their nests with digging sticks of the same kind used for digging tubers. For digging in soft sand or wet mud, baler shells were excellent implements and were still in frequent use in the 1980s.

A baler shell on the ground was a common sign of the presence of a well. Although potable surface water was abundant in the wet season, it was not so in the dry season, except inland beyond the extensive tidal limits where permanent lagoons or the perennial streams of the Archer and Kendall Rivers provided fresh water. Coastal people preferred to dig a well, even next to a large pool of water (Fig. 7). The most preferred water was that occurring in the aquifers of ridges based on shellgrit. This water is nearest the surface, clears quickest after the water level has been dug out, and tastes sweetest. Next is sandridge water, followed by water which has to be dug in muddy soil. Considerable etiquette and religious formality (and, occasionally, vehemence) accompanies the digging



FIGURE 9. Morrison Wolmby, Noel Peemuggina and Alan Wolmby standing with spears, Aayk (Cape Keerweer area) 1976. Photo: Peter Sutton.

of wells. Ancestors are informed of who is present, requested to do no harm to the diggers, asked to make the water come close to the surface, and so on.

Along the coast, fish, sharks and rays were a major food source. The actual Gulf beaches were not as attractive as the peri-coastal waterways and much if not most fishing seems to have been done in tidal reaches, estuaries and lakes. A good deal of this fishing in earlier times involved the use of drives, of weirs or fences across waterbodies, of vegetable stupeficients (for example, the bark of the baubinia *Cathormion umbellatum* (Vahl) Kosterm., and *Ormosia ormondii* (F. Muell.) Merrill), of a variety of nets (ovate, reinforced with a cane withy), or of three- or four-pronged spears. Rolled melaleuca bark provided a torchlight for luring, confusing and illuminating fish during night hunting. Women occasionally speared fish but spears in general were men's equipment. Multi-pronged spears, barbed with bone or, more recently, nails, have generally given way to wire-pronged spears for obtaining marine species, and shotguns and .22 rifles had, by the 1970s, generally replaced

spears for birds, pigs and wallabies. The old wooden-pronged spears were used for spearing birds and mammals as well as marine species (Fig. 8), and some of the single-pronged spears were used for fish, so it is impossible to claim that hunting spears were highly specialised. A very common spear type was the hardwood-headed spear with a double-pointed single barb of bone (later steel). This was used mainly for bigger land game but also for fishing (see e.g. Thomson 1939a: 210, McConnel 1953: 26). It is possible, though, to differentiate between spears for hunting and those specifically made for fighting (see below), even though, in an affray, any handy projectile might be used. In the 1970s in the Cape Keerweer region this author saw a stingray 'speared' with a long-handled shovel, fish 'caught' in a creek with shotgun blasts, and a *Varanus goanna* felled by thrown sticks gathered from the ground on the spur of the moment. Similar improvisations were probably resorted to in earlier times as well. Catching certain marine creatures by hand was a prized skill, although some sluggish fish in drying pools of water were an easy catch. Water birds are said to have been caught by swimmers



FIGURE 10. Man repairing spear point, Archer River, 1930s. Photo: U. McConnel.

pulling them underwater. More often the men, disguised with mud, and with only their nostrils and forehead above water, would swim slowly among the birds before startling them into flight. A number could then be brought down with a single spear or a couple of sticks.

Large quantities of spears, most of them well over two metres in length, were a distinctive mark of a western Cape York traditional camp (see Thomson 1939a Plate 23: lower, and Fig. 9 here). Spear-making (and constant repairing) was a major occupation for middle-aged and older men (Fig. 10), and in the 1980s continued as a source of income. The problem of marketing spears through the craft outlets was diminished by the introduction of

detachable sections. Traditional spears were sometimes made in three sections, and commonly in two, so the adaptation was not a major one. The sectioning was designed to yield an optimal combination of lightness, strength and flexibility. It must be remembered however that, in use, spears were essentially fragile and frequently broken or damaged.

Whenever possible, spears were propelled by the use of the distinctive Cape York Peninsula spearthrower with its long, slender body, baler shell balance, attached peg, and occasional decorations of *Abrus* seeds and yellow orchid stem binding (Figs. 8, 11). A lightweight version capable of floating was sometimes used when on the water, and a 'false

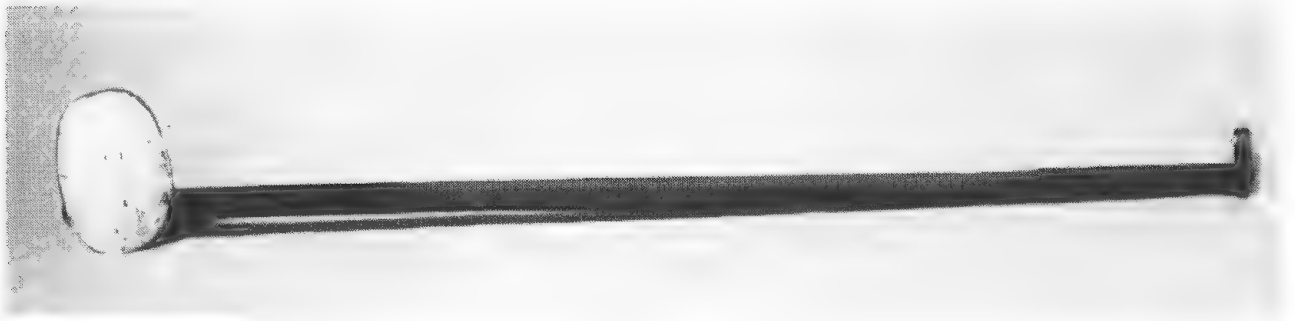


FIGURE 11. Spear-thrower made in 1977 by Clive Yunkaporta, Peret Outstation via Aurukun.

woomera' was used in conflict (see below).

The inland economy was dependent on fewer vegetable staples and a narrower range of other vegetable foods, rather widely dispersed. It was also focused on freshwater lagoon and river fish and shell species and on reptiles. Apart from kangaroos and emus, which could not be relied upon as an obtainable protein source from day to day, possums and bandicoots would have been among the larger animals in the diet. By contrast, the coastal economy offered not only more variety and greater concentrations of foods, but also more abundant large-bodied animals such as the wallabies of the dune systems, the sharks and rays of the estuaries, and, since the 1920s, feral pigs in large numbers.

Cultivation and domestication

In pre-mission times people optionally left *in situ* the stem and vine of a tuber they were digging out so another would grow on the same vine. In the 1970s this was still occasionally the practice. By the 1970s, cultivation of introduced food-bearing plants such as watermelon, bananas, pawpaw (papaya), cassava and coconuts was also occurring in very small plots near outstation camps or planned outstation sites, as well as here and there in the Aurukun village itself. The ravages of vermin, dogs and children, problems with water supplies, and the intermittent absence of the garden's personal cultivator, frequently led to these gardens falling into disuse. Much of their function was to act as symbolic claims on place, or as signs of diplomatic intent towards Europeans, who have so often expressed a desire to see Aborigines interested in agriculture. The slightness of their production was not critically important.

As elsewhere in Australia, camp dingoes were quickly replaced with European dogs and large numbers might become attached to Aboriginal households in the area. Dogs continued to be regarded as kin and to bear an array of clan-totemic names at least well into the 1980s, although most also acquired English names. They, like their predecessors, were of continuing use as watchdogs

and of occasional use as hunting aids, and they remained kin.

By the 1970s piglets had become gifts and some survived to become members of camps, at least in remote places such as Ti Tree. Their tendency to bully humans for food can become rather alarming by the time they reach full adult size and they sometimes meet untimely ends at that stage.

European cats are occasional pets but their feral cousins were not prime hunting targets as they are in much of desert Australia. Those kittens which survive the attentions of small children might develop a loose relationship to certain households but do not achieve the valued status of dogs. They lack precedent.

Horses and cattle formed a focus of work and life for many Wik people for much of the mid twentieth century, although care and maintenance of herds, fences, plant and equipment were intermittent and depended on a small number of dedicated Aboriginal stockmen and occasional European managers. While the strong arm of the mission was in charge, the Aurukun cattle industry turned off beasts, barging them out off the coast or walking them overland as far as the railhead at Mungana some 400 kilometres to the southeast. In the 1980s, after the cattle operations had been in disarray and decay for a decade or more, Aurukun Community Incorporated organised the eradication of cattle from the Aurukun Shire as part of the Australia-wide brucellosis and tuberculosis eradication campaign.

Food preparation and consumption

While heavy game might be transported tied to a long pole carried by two people, under bush conditions most foods were carried in woven bags or in containers made from hardwood bark (Fig. 12). Food was also wrapped in paperbark (from *Melaleuca* spp.) and tied with vines or grass, both for transportation and warming near a fire. Paperbark is in fact the commonest and most versatile natural material in the western Cape York traditional subsistence kit (Figs. 13,14). The uses of paperbark extend well beyond subsistence, but



FIGURE 12. Women with heavy loads, Archer River, 1930s. Photo: U. McConnel.

because of its special role in cooking and eating we will deal with all of its uses here.

Paperbark is used as a food preparation surface on which meat can be sliced or a damper kneaded (Fig. 15), a coverlet to shield food from flies or dogs, a source of kindling when outer barks and grasses are wet, a heat-sealing medium for meats in earth ovens, a mitt with which to pick up steaming hot foods or billycan handles, a platter from which to eat, a towel with which things are wiped, a lightly

abrasive cleaner (when crumbled) for greasy or blood-covered hands, a clean, dry surface to sit or sleep on, a blanket to sleep under, a shroud in which to mummify and transport corpses, a roofing material for shelters, a torch for night travel or fishing, a pouch for containing stingray barbs or small medicinal or magical substances, a cigarette paper, a binder for awl handles, a napkin for babies, a menstrual pad, and a sheet of toilet paper. Its abundance in coastal swamp areas is one of the



FIGURE 13. Stripping paperbark from a melaleuca tree, Archer River, 1930s. Photo: U. McConnell.

factors which makes the coastal region such a convenient place to live, compared with the inland. The preferred species provide sheets of soft, durable material which are easily prised from the tree with a sharp stick, which impart little or no odour or taste to food and which leave no sharp or stringy fragments behind when fragmenting.

Most cooking was carried out by simple broiling on an open fire, or by the earth oven technique. Shark or ray liver, however, might be fried in a baler shell, or lightly cooked before being wrapped in the washed white flesh of the shark or ray and then tied up in paperbark to be slowly warmed through at the hearthside. This distinctive loaf of high vitamin and protein content gives rise to the term by which most Wik people refer to the elasmobranch (sharks and rays) category: 'tying meats' (for example, *minh katheng* in Wik-Ngathan). The sign for the same category is the wringing of hands, a reference to the squeezing of white fluid from the flesh after cooking and before eating.

The earth oven technique was used for large game, but also for large quantities of small game such as marsupial mice and fruit bats or vegetable foods such as tubers. The following description of that method is probably only strictly true for the coastal region, where there is no stone. (Note also that other cooking practices varied within the region: inlanders cooked the tuber known as *angk* (Wik-Mungkan) or *walken* (Wik-Ngathan), probably a *Cayratia* sp., in the earth oven, but coastal people roasted it in the coals; some coastal clans half-cooked stingray livers, while others placed them raw inside the white flesh. These differences were



FIGURE 14. Carrying sheets of paperbark, Archer River, 1930s. Photo: U. McConnell.



FIGURE 15. Paddy Yantumba removing eggs from a file snake, Big Lake 1976. Photo: Peter Sutton.

consciously maintained as an aspect of local group identity.)

To make an earth oven, a pit was dug and a vigorous blaze lit in it (Fig. 16). On this fire, or one nearby, the fur, skin or scales of the beast were singed away and the burnt fragments lightly scraped off. Lumps of termite mound, if available, were thrown into the pit to get hot. (The earth oven technique is known as '(burying) in termite mound'.) Where there was no termite mound - whose heat-holding properties are exceptional - lumps of shellgrit were used. At the bottom of this hierarchy of oven bricks was swamp mud, a last resort when the other two substances could not be had. Termite mounds are thus a factor in defining optimal campsites in the region.

When the oven bricks were hot, they were covered in green leaves on which the meat was placed skin-side up. Large sheets of paperbark (or, in the 1980s, corrugated iron if available) were then placed on the meat and the whole oven was sealed with sand. The relative ease with which the pit could be dug and the oven properly sealed depended on the presence of sand, and the whole process usually required access to suitable paperbark trees, which were thus further factors in defining a good campsite location. Earth ovens were usually near, not right on, overnight and base camps. They accumulated quantities of offal, skin, feathers and bones which made the immediate area unpleasant for camping. The termite mound lumps were re-used until fragmented, on subsequent visits to the site.

Limited food storage was practised. Nonda plums



FIGURE 16. Earth oven cooking, Watha-nhiin Outstation, 1976. Photo: Peter Sutton.

(*Parinari nonda* F. Muell. ex. Benth.) were dried on the rooves of shelters, or collected dry from the ground (the dry form even has a different name), and were kept for some weeks after their season of superabundance. Long yams (*Dioscorea transversa* R. Br.) were stored in the sand for weeks and even months (Sutton and Smyth 1980). Long-necked turtles might survive a day or two trussed up, and in the Big Lake area barramundi is said to have been cooked, wrapped in paperbark, and buried in the cool earth for eating days later. Most food, however, was eaten within twenty four hours.

Food preparation was elaborate in the case of vegetable foods with toxic or unpleasant properties which required scraping, pulverising, leaching and sieving (for example, the round yam *Dioscorea sativa*, the arrowroot *Tacca leotopetaloides* (L.) Kuntze, or the mangrove fruit *Avicennia marina* (Forssk.) Vierh.). These were not preferred foods and by the 1970s most had become just a hardship memory. Nonda plums were pounded and mixed with water to make a kind of fruit soup (Thomson 1939a), much favoured by children and by the toothless. A wooden mallet and pounding board were used in these processes, and mashed food was collected in large messmate bark containers (Fig. 12). This same bark (from *Garcinia warrenii* F. Muell.) was also used for canoes, sleeping platforms, and inland shelters. It is a characteristic

resource of the hinterland behind the narrow coastal floodplain.

Foods were mixed in earth ovens in order to create changes of flavour, and some non-foods were used as condiments in the same context. For example, the leaves of two eucalypts known in English as 'bloodwoods' (but named separately in Wik languages) were placed in earth ovens with the meat of game such as wallaby or wild pig to improve their flavour. This attention to culinary detail marks the culture of this kind of region as very different from, for example, the cooking styles of people of the Western Desert.

Travel and transport

By further contrast with inland peoples, and especially those of desert Australia, in pre-settlement times Wik people were comparatively sedentary, making less frequent shifts of camp and travelling much shorter distances between camps. Base camp shifts were usually about five or six kilometres only. People were therefore able to carry more possessions, and lived in an environment rich in a wide variety of raw materials from which artefacts might be made. It is not surprising, then, that the inventory of their material culture is relatively large.



FIGURE 17. Noel Peemuggina and Johnny Ampeybegin drinking from baler shells at the beach near Big Lake, 1976. Photo: Peter Sutton.



FIGURE 18. Woman weaving basket, Archer River, 1930s. Photo: U. McConnel.

Message sticks, which were small tablets of wood carved with non-figurative symbols representing days of travel, places, people or commodities, were carried by messengers when arranging meetings or other dealings, both ceremonial and secular (McConnel 1953, Sutton 1978: 93–4).

The variety of containers used to transport or hold things in this region was, perhaps, exceptional. In addition to the woven bags and baskets discussed below, and the bark containers discussed above, there were the ubiquitous baler shell (used for drinking (Fig. 17), digging, baling and cooking as well), the conch shell and bamboo tube (for transporting water), the palmleaf cup, and the

carved wooden vessel (see Thomson 1939a: Pl.XXI, 1939b: 85).

In the 1980s women of the Wik peoples were still making a variety of differently shaped woven bags and baskets employing many different fibres and weaves, and a number of natural dyes (see Adams 1986, McConnel 1953, Thomson 1939a). These were used not only for carrying things, but also for sieving and leaching bitter foods, for hanging valuables high above the reach of children and dogs, for imparting a militant spirit to small boys (by smacking woven bags against their calves), and, in the case of larger woven baskets, as cradles for babies. Woven containers were also a focus of traditional religious symbolism (there was a Woven Bag totemic clan, for example) and, because of their frequent use as gifts, they were an important medium for maintaining good relations between individuals and groups (Figs. 18,19).

The two main types of watercraft were the simple 'floating log', most frequently used during brief river crossings, and the messmate bark canoe. From the Archer River north, dugout canoes were made from the cotton tree and used for hunting sea turtle and dugong in the Gulf waters. Canoes were used on the inland lakes, swamps and estuaries during and just after the wet season, particularly for collecting eggs of the magpie goose, which are superabundant at that time, and for spearing fish. They were both paddled and punted. Figure 20 shows a canoe made and used for egg collecting in the Munpun area in the wet season of 1975-6, and then abandoned. That may have been one of the last traditional uses of a canoe in the region, as aluminium dinghies have become commonplace and store foods have increasingly replaced bush foods.

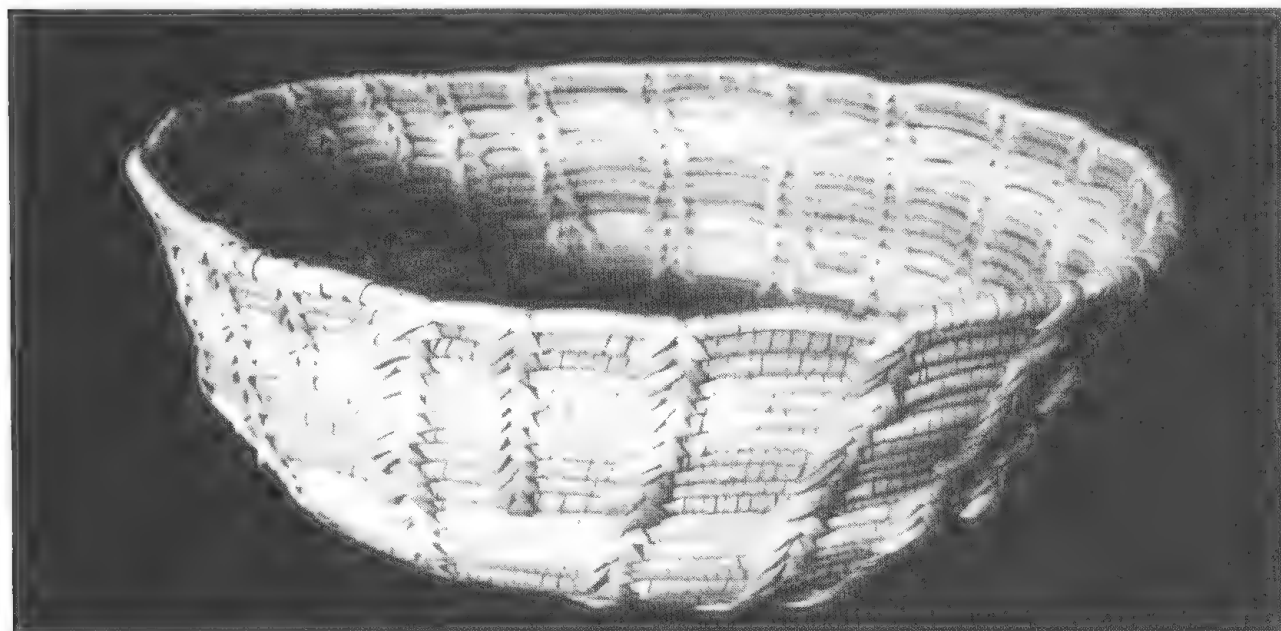


FIGURE 19. Basket made by Isobel Wolmby from Aurukun. Collected by P. Sutton, 1986.



FIGURE 20. Disused bark canoe near goose-egg swamps, Munpun 1976. Photo: Peter Sutton.

Fighting and duelling

Women fought with yamsticks and men fought with spears and spearthrowers, particularly if the conflict took place among those who had had time to prepare for this important aspect of individual and group relationships in the region. A 'false woomera' was also used by men - this was a spearthrower lacking a peg or baler shell ornament or both - and was used as a club. Spears for fighting at a distance were shorter and unbarbed. Long fighting spears were used for closer combat and for jabbing in the thigh as a means of settling grievances (see McConnell 1953: 25-6). Some of the spears specifically made for fighting had a cluster of stingray barbs at the nose, all pointing forward.

These made an extremely painful and messy wound (Fig. 21). Men's clubs were either long and pointed, like yamsticks, or short, knobbed and pointed, and were used both for impact and for fending off spears (Fig. 22). The long throwing stick was also used to deflect spears. Shields were not used in this area. The proboscis of a sawfish or the teeth of a shark would be set in a handle of milkwood (*Alstonia actinophylla* (A. Cunn. A. Schum.)) to form a fighting sword. The conflict-related part of the material culture array in this region was clearly highly elaborated.

By the 1980s conflict was carried on primarily with fist-fighting and the opportunistic use of objects at hand which might be turned into weapons, such as pieces of fence, billycans, bottles,

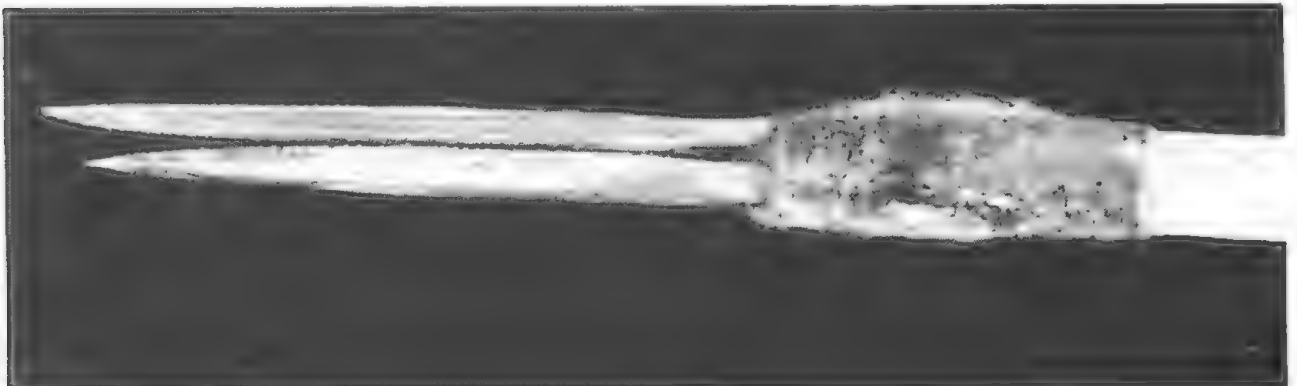


FIGURE 21. Spear-head showing sting-ray barbs, made in 1977 by a Wik man, Peret Outstation.

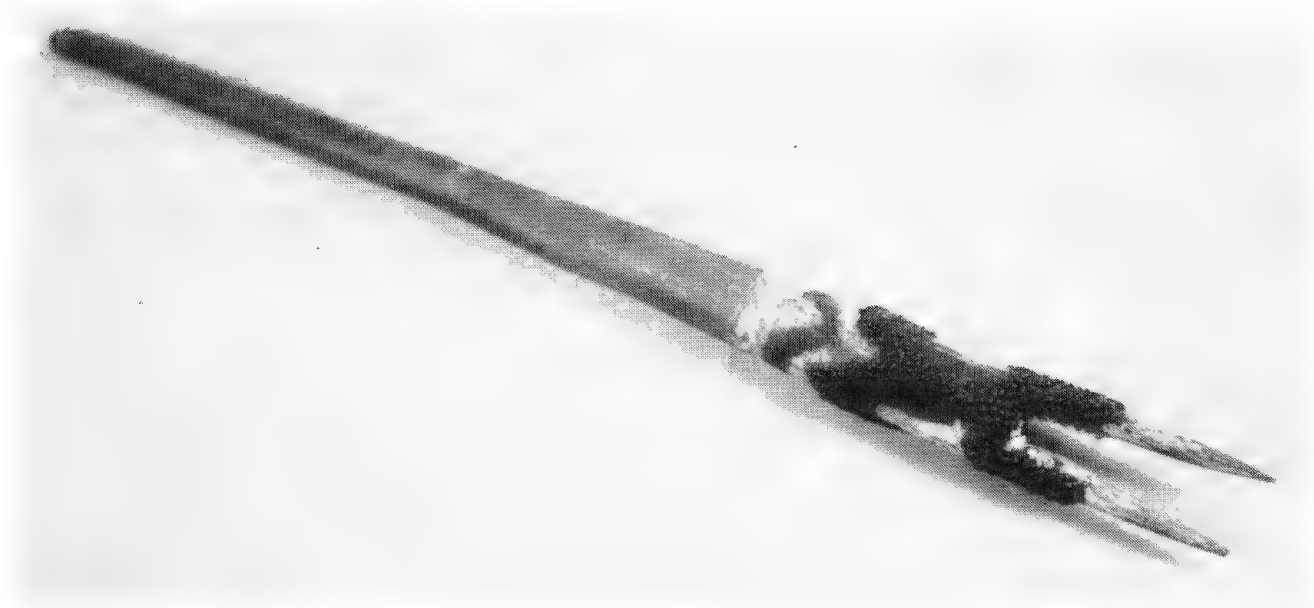


FIGURE 22. Two-pronged wooden club, decorated with seeds traded from Torres Strait, used to parry spears, Archer River, 1930s. Collected by U. McConnell.

broomsticks, steel knives and, occasionally, rifles or shotguns. By the early 1990s spearings had become rare.

Manufacturing technology

Tools used in manufacturing traditional artefacts included knives (originally made from shell, especially mudshell, or from bamboo, but latterly of steel), shell drills for boring holes in necklet shells, axes made of stone or steel, paired sticks used to tie the two sides of bags during weaving, bone awls used to pierce bark for canoe-making, wallaby incisors (still in the jaw) for cutting and graving, and a 'palette' or resin bat made of ironwood, with a wallaby incisor set in its handle, which was used for smoothing heated resin or wax and for engraving (Fig. 23). Woodrasps, saws, hammers and nails, heated wires, sharpening stones and butcher's

'steels' were all in regular use by a cross-section of Wik peoples by the 1970s. Carpentry and basic mechanics' skills were taught by missionaries and other community workers and a wide range of workshop tools were available in the main population centres from about the 1930s.

Magic and medicine

As in many parts of Aboriginal Australia, ironwood smoke (using the leaves of *Erythrophleum chlorostachys* (F. Muell. Baillon) in this case) was used to send away the spirits of the dead. After scraping, the roots of a fern (*Drynaria quercifolia* (L.) John Smith) were burned to yield a smoke which would send people into a deep sleep so one could, for example, steal away from one's family at night to engage in sexual activity. One could make oneself invisible (for example, when seeking

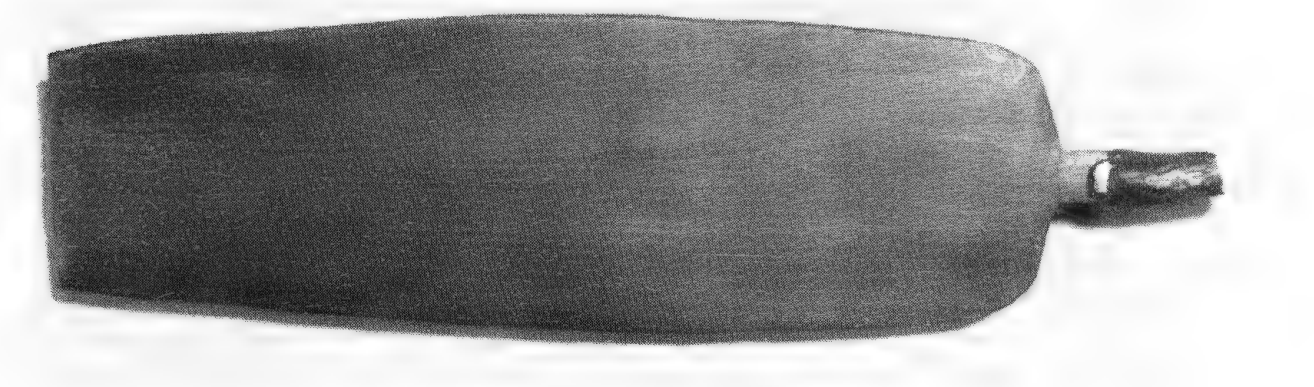


FIGURE 23. Ironwood palette used for smoothing heated wax and as an engraving tool, with wallaby tooth incisor attached. Collected by U. McConnell, Archer River, 1930s.

revenge) by tying one's upper arms with a string made from the roots of a fig (*Ficus virens* Aiton ex Dryander) or with the grass called *keent* in Wik-Mungkan (Family *Gramineae*). Rain could be prevented by burning the leaves of the whitefruit (*Eugenia eucalyptoides* F.Muell.), or by burning the roots and branches of the deciduous hardwood known in Wik-Mungkan as *yuk kuk* (possibly *Tinospora minasira*). Gamblers could improve their luck by secreting on themselves pieces of the bark of *Excoecaria parviflora* Muell. Arg., or of the 'crocodile-hand tree' (*Terminalia subacroptera* Domin.). These and other magical substances come under the same cover-term as materials used for both healing and sorcery in each of the Wik languages (for example, *operr*, Wik-Mungkan, and 'medicine' or 'bush-keymas [chemist]' in English, although the Pacific pidgin loan *purriy-purriy* is used for sorcery items).

Magical procedures in this region were complex, and too many to give in full here. One example is the transformation of wooden effigies or real specimens of small reptiles into live saltwater crocodiles which were then owned and controlled (and considered 'sons') by particular older men. The effigy or lizard would be bound with string and smeared with blood - preferably human - before being released into the water with appropriate exhortations. On returning to camp, the crocodile man (*pam thikel-kathenh*, 'man crocodile-ties' in Wik-Ngathan) must bring home very large pieces of firewood, not small ones, otherwise the crocodile would be undersized. These men are said to have called up their personal crocodiles and to have stood in the water with them, cleaning their teeth with a twig. The crocodiles could be sent to the river of another group to kill people. Deaths from crocodile were normally attributed to the malevolence of others.

Ceremonial life

Ceremonies in the area involve elaborate carvings made of wood, hair, bone and many other materials (see McCarthy 1964, 1978; Berndt, Berndt & Stanton 1981; Morphy 1981; Sutton 1988; Bartlett 1989). These are among the most spectacular sculptures in Aboriginal Australia.

While they are highly traditional in meaning, and carved and painted totemic wooden objects were collected from the region at the earliest stages of contact, in their present elaborate form the Aurukun sculptures appear to have flourished mainly since the advent of steel tools and the introduction of techniques such as morticing during the mission period in the present century (see McCarthy 1964: 300). These more technically complex works

probably do not pre-date the late 1940s, when a major collection of them was made at Aurukun and lodged with the University of Queensland (now in the Anthropology Museum, Department of Anthropology and Sociology). The many examples filmed in ceremonial use at Aurukun by the Australian Institute of Aboriginal Studies in 1962, and collected by Fred McCarthy, are now in the National Museum of Australia (Dunlop 1964, McCarthy 1978). Although they were still being made for ceremonies in the 1990s, and some had been given to outside individuals or institutions (such as the South Australian Museum), only rare examples were allowed to reach the market.

These sculptures are used in regional cult ceremonies, a highly competitive form of religious celebration in which events from local mythologies are enacted by dancers to the accompaniment of songs and symbolic cries. They are, among other things, statements about rights and interests in specific places. They refer to the mythic 'title deeds' of Aboriginal customary law, and their making and use in performance by particular people wearing particular body-paint designs have strong local political and territorial meanings, as well as spiritual and aesthetic aspects. They may be spiritually dangerous for some time after their manufacture and are usually allowed to rot away in the bush.

Most Aurukun sculptures are figurative representations of particular beings in the myths, and are generally long and gracile, ranging from around 400 mm to over two metres in length (published illustrations are in e.g. McCarthy 1964, Morphy 1981, Berndt, Berndt & Stanton 1982, Sutton 1988). They are painted in non-realistic bands and patches of colour, and show a distinctive degree of trouble taken to insert realistic (and sometimes real) teeth, spines, tails and fins into the figures. They lack the smooth, static formalism and inscrutable stolidity of a good deal of the carving associated with some other so-called tribal societies. They have a stark, unpredictable and dramatic look which appeals especially to lovers of modernist 'primitivism'.

More restricted ceremonial material cannot be reported on here (cf. McConnel 1953), but it is appropriate to note that, according to initiated men alive in the 1970s, a previously unreported drone tube was in regular use at initiation ceremonies up to the late 1960s, although none have been collected to the author's knowledge. Percussion accompaniment to singing was mainly done by clapping. Saliva was regularly licked onto the hands to increase the clapping volume. Performers wore iridescent pendants cut from mother of pearl or nautilus shells, which were smeared with red ochre. They also wore filaments of white cockatoo feathers joined at the stem with a resin/wax mixture,

armbands of red-ochred pandanus, and sometimes armbands and girdles made from bark studded with red *Abrus* seeds. Some of these ornaments were also used in daily life.

When performing 'Island Dance', a dancing and singing style based on an amalgam of Pacific Island traditions with those of Cape York Peninsula, dancers in recent decades have worn and carried matchbox bean rattles, and sported colourful cotton *nagas* (loincloths) or synthetic grass skirts. Rhythm for this style is provided by hand-drumming on a membrane stretched over the end of a wide cylinder (often an inner tyre tube on a length of plumber's polythene pipe), or by beating of sticks on a metal flour drum. In the earlier part of this century, cylindrical drums were only used north of Archer River (McConnel 1953: 23). By the 1980s women had added a very erotic version of Polynesian hula dancing to their repertoire, which required flowers in the hair, leis, and brightly coloured synthetic grass skirts (Lurex is desirable). But hula here is only performed at mortuary ceremonies.

Personal adornment

Before adopting western dress, Wik people basically went naked, although women wore string aprons for symbolic or ritual reasons at certain times (see McConnel 1953: 15). People did wear many ornaments though, including pendants of shell and

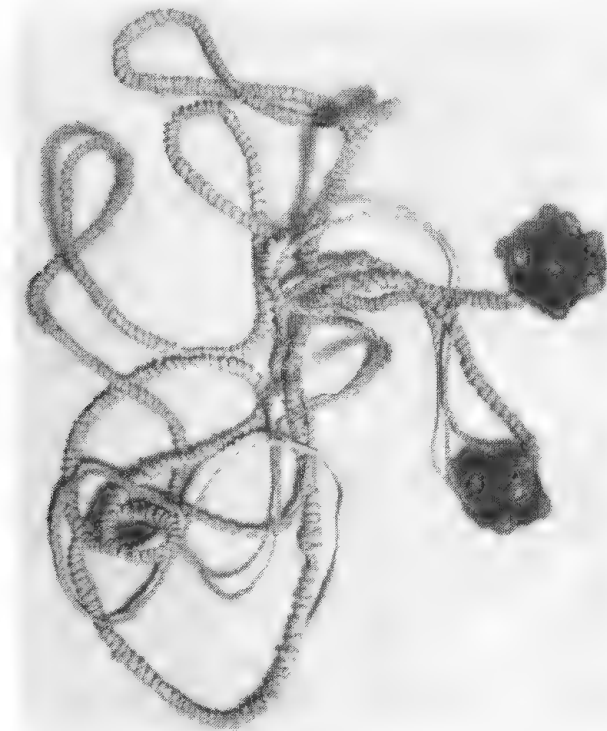


FIGURE 24. Widow's necklet, with beeswax pendants studded with *Abrus* seeds. Collected by U. McConnel, Cape York Peninsula, 1930s.

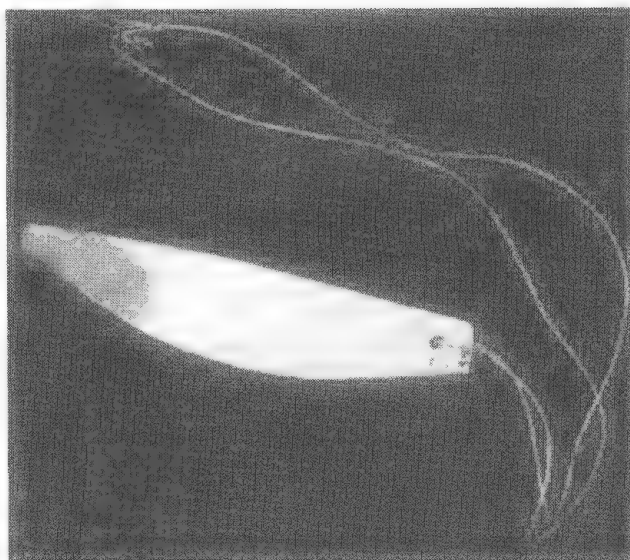


FIGURE 25. Shell pendant made by George Sydney Yunkaporta, 1977, Watha-Nhin Outstation. Collected by P. Sutton.

beeswax, shell nosepegs and wooden earlobe cylinders, strings and girdles of hair, fur, feather down, orchid-bark, palm fibre string, fig pneumatophore string, and threaded cowrie shells, pearlshell pieces, grass-bugles and *Abrus* seeds (Figs. 24,25). These adornments reflect an aesthetic preference for white and shining objects, or red objects. White clay and red ochre are also the dominant colours of ceremonial body paints in the region.

Aboriginal footwear is usually associated mainly with desert groups, but this author has been told on reliable authority that Wik people in the past did make grass and string sandals. Anyone who has tried to walk on the region's hot dry sands in bare feet will understand why this may well have been so. Local languages have an autogenous term for footwear (*tha' morrok*) which may have originally referred to the sandals but now refers to shoes and boots.

Drugs

Thomson (1939b) came to the view that tobacco had been available, but not grown, in Cape York Peninsula for a very long period before his first visit there in 1928. He reported three kinds of smoking pipe. One was a long cylinder, usually of bamboo or ironwood, open at one end into which someone smoking a cigarette or pipe expelled smoke which was at the same time inhaled by someone else through a small hole near the other end. Another was a short, broad cylinder of bamboo or ironwood which was filled with smoke then passed around to others who inhaled and exhaled the same smoke

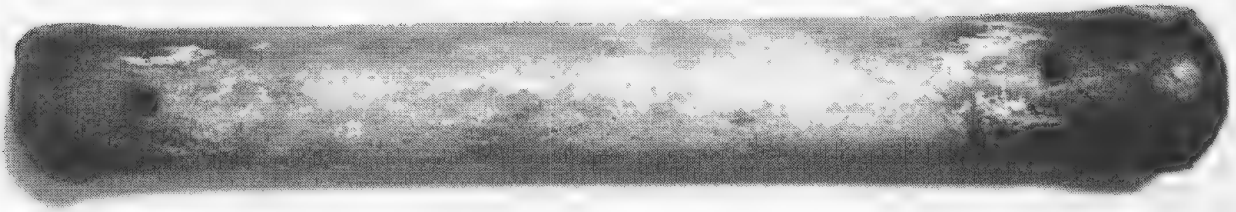


FIGURE 26. Communal smoking-pipe, collected by U. McConnel, Archer River, 1930s.

(Fig. 26). The third was modelled after the English briar-pipe, made of a very hard species of wood, and bored out with a hot wire. This last type was the only one still in regular use among the Wik peoples by the 1970s, although cylinder pipes were still made for the Aurukun craft shop.

Material culture today

At the present time most Wik people live for most of the year in modern Queensland-style houses or the tin sheds of outstations, and move about by Toyotas, cars, planes and tractors or motor-powered boats and, occasionally, horseback. Television sets and videos have become common possessions. Some Aboriginal households have acquired telephones. While traditional ceremonies are maintained in an attenuated form, Island Dance, hula and rock'n roll have become more frequently performed. The dead are no longer mummified, carried about for long periods or cremated at elaborate ceremonies, but are buried with a simple Christian rite and their houses ritually 'opened' by a mixture of traditional totemic and modern secular performances. Their spirits are still ritually sent to their homelands and their names are still prohibited from public use for a period after the death.

By the 1980s, the Wik economy had become based largely on welfare payments and limited local employment on community services, although fish, pigs, crustaceans and water birds still provided significant proportions of the diet. Alcohol had

become a major economic and social preoccupation. Rifles, shotguns, nylon fishing lines and steel hooks had replaced most kinds of traditional hunting equipment, although the multi-pronged wire spear and spearthrower were still used for shoreline hunting. A number of bush medicines were still used, but constant use was also made of western medicines obtained through community hospitals and health workers. Many traditional items of material culture, and some objects introduced by missionaries (such as feather flowers and pandanus place-mats and bowls), were still made, however, either for the cash available from the craft outlets (see Adams 1986), or for gifts within the community.

ACKNOWLEDGMENTS

My chief debt is to the people of the Cape Keerweer region, especially the residents of Watha-nhiin and Aayk Outstations in the years 1976–1979. Noel Peemuggina, Isobel Wolmby, Ray Wolmby, Clive Yunkaporta and Peter Peemuggina were my main informants on the specific matters dealt with here. I also wish to thank Dermot Smyth for making the botanical collections and for his cheerful company over many weeks of arduous field work. Dermot Smyth and The Queensland Herbarium provided the botanical identifications. I thank the South Australian Museum for permission to reproduce Figures 3–8, 10, 12–14, and 18, and the Museum's photographer, Trevor Peters, for Figures 11, 19, and 21–26. Funding for field work was provided by The Australian Institute of Aboriginal and Torres Strait Islander Studies, the Australian Department of Education, and the University of Queensland.

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THE CHOOKOONING METEORITE : A NEW (L6) OLIVINE-HYPERSTHENE CHONDRITE FROM SOUTH AUSTRALIA

M. ZBIK & A. PRING

Summary

The Choolkooning 001 meteorite is a single stone of 1.977 kg found approximately 63 km north of Hughes, South Australia, in 1991. It has been classified as an L6 chondrite shock facies S3-4 and contains olivine (Fa_{24.7}), orthopyroxene (Fs_{20.5}), plagioclase (An₁₂ Or_{6.2}Ab_{81.8}), clinopyroxene, nickel-iron, troilite, chlorapatite and chromite. Mineral composition indicate that Choolkooning 001 was a metamorphosed part of the L-planetoid and was moderately shocked before reaching Earth.

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ZBIK, M. & PRING, A. 1994. The Choolkooning 001 meteorite: a new (L6) olivine-hypersthene chondrite from South Australia. *Rec. S. Aust. Mus.* 27(1): 53–56.

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M. Zbik and A. Pring, Department of Mineralogy, South Australian Museum, North Terrace, Adelaide, South Australia 5000. Manuscript received 9 December, 1992.

A single mass of the Choolkooning 001 meteorite, now in several pieces, was found by an unknown collector, 30 km west of Choolkooning Rockhole and 63 km north of Hughes on the South Australian part of the Nullarbor Plain. The approximate co-ordinates for the site are 29°55'S, 129°50'E. The broken and weathered fragments, total mass about 2 kg, were illegally collected and exported to the United States of America in 1991. The meteorite was purchased in the United States of America by an Australian mineral dealer, Mr Robert Sielecki, who surrendered it to the South Australian Museum upon his return to Australia in March, 1992.

In recent years the Nullarbor Plain has proved to be a productive area for the recovery of meteorites (Bevan 1992; Bevan & Binns 1989a, 1989b) and in the last few years has attracted the attention of illegal meteorite collectors. Under legislation enacted by the Governments of Western Australia and South Australia all meteorites found in these states are the property of the Crown. An unfortunate consequence of the illegal trade in meteorites is the loss of important information on the exact date and location of the find. The locality given for the Choolkooning 001 meteorite by the dealer from whom Mr Sielecki purchased the stone was 100 km north east of Deakin, Western Australia. This places the find site within South Australia, approximately 63 km north of Hughes, some 30 km west of Choolkooning Rockhole (Fig. 1). In accordance with the guidelines on the nomenclature of meteorites from the South Australian Nullarbor (Bevan & Pring 1993), the meteorite has been named Choolkooning 001, being the first meteorite to be recorded from the Choolkooning area.

PHYSICAL DESCRIPTION

The meteorite is in eight fragments which range in size from 5 cm in length up to 20 cm. Four of the fragments fit together to form an incomplete rounded stone, two other fragments also appear to be part of this stone, but the other two fragments may be pieces from another mass of the meteorite. It is clear that several fragments are missing and it is not possible to say with certainty whether the meteorite was originally one or two stones.

Each piece shows a dark brown 1 mm thick fusion crust on at least one surface. The stone is heavily weathered displaying iron staining of silicate minerals and fractures filled with iron oxides. The broken surfaces of the fragments are also heavily weathered and the fusion crusts of some fragments are encrusted with calcrete, indicating that the meteorite had been exposed to the weather for many years. The interior of the meteorite is grey in colour and medium to fine grained.

In thin section the meteorite is generally light coloured with heavy iron oxide staining in some patches (Fig. 2). The chondrules are recrystallised and have poorly defined boundaries but are recognisable under crossed polars. They are typically 0.5 mm in diameter but some measuring up to 4 mm in diameter were also noted. Metal and troilite occurs as finely disseminated grains throughout the matrix. One piece of the meteorite was cut and the surface polished, and a polished thin section was also prepared and used for petrographic examination and in electron microprobe analyses.

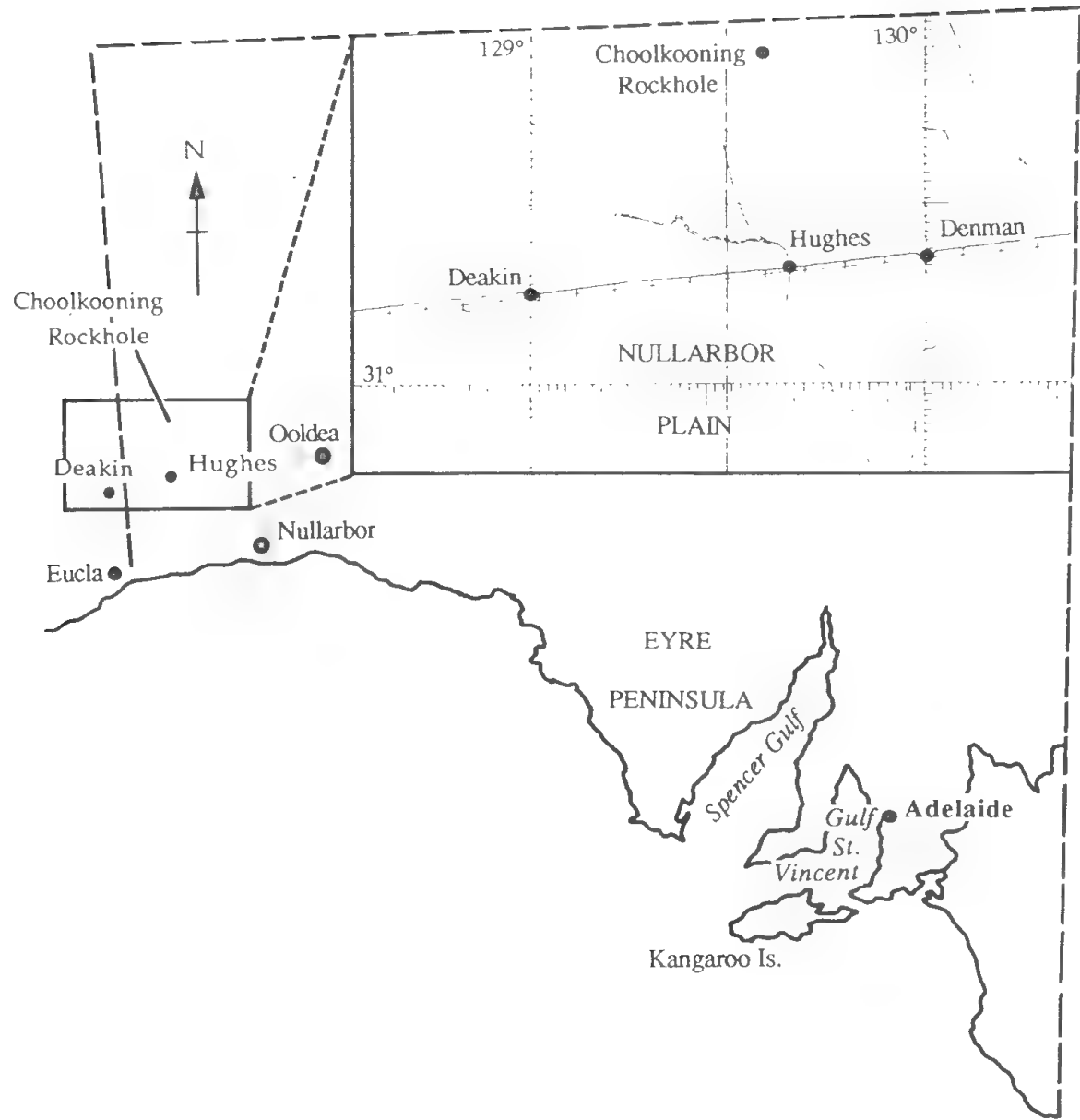


FIGURE 1. Map of South Australia showing the approximate location of the Choolkooning 001 meteorite.

TABLE 1. Average chemical compositions of major minerals in the Choolkooning 001 meteorite.

oxide	weight %		
	olivine	orthopyroxene	plagioclase
SiO ₂	39.1	54.1	63.8
TiO ₂	0.1	0.2	0.1
Al ₂ O ₃	0.1	0.1	21.0
FeO	22.8	14.7	0.6
MnO	0.5	0.5	0.1
MgO	38.8	28.8	0.1
CaO	0.1	0.7	2.3
Na ₂ O	—	—	8.5
K ₂ O	—	—	1.0
Cr ₂ O ₃	0.1	0.1	—
NiO	0.1	0.1	—
Total	101.7	99.3	97.5

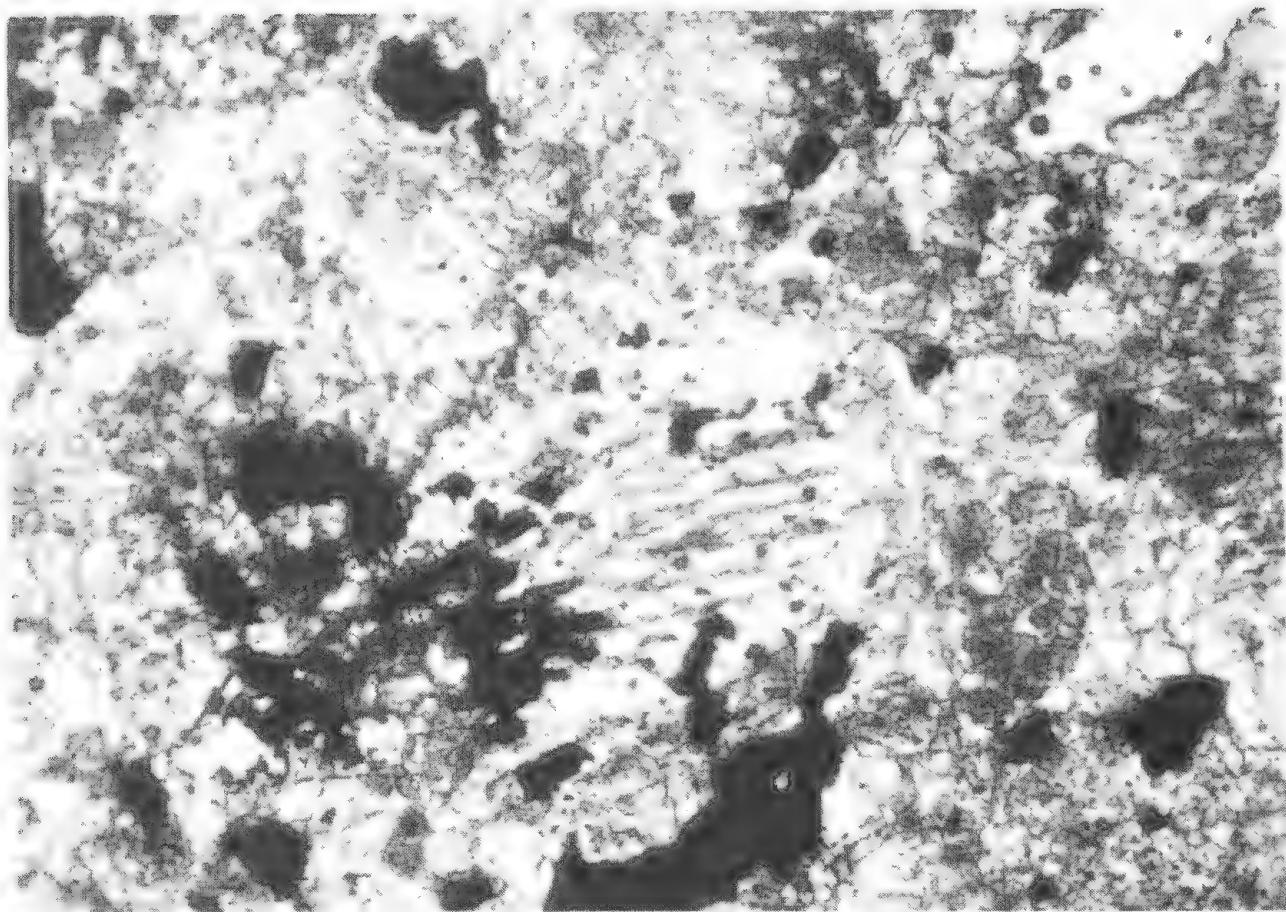


FIGURE 2. Photomicrograph of the Chookkooning 001 meteorite in thin section showing typical fractured olivine grains in the recrystallized matrix.

MINERALOGY

Compositions of the silicate minerals were determined with a JEOL electron microprobe at the University of Adelaide Centre for Electron Microscopy and Microbeam Analysis. Analyses were made using an accelerating voltage of 15 kV, a sample current of 3 nA, and a beam width of 5 μm . Representative mineral analyses are presented in Table 1.

Relic chondrules and chondrule fragments are composed predominantly of olivine, with lesser amounts of orthopyroxene. 'Barred' chondrules composed of olivine and orthopyroxene also have thin lamellae of either clinopyroxene or plagioclase. The matrix consists of olivine and orthopyroxene grains with very rare grains of clinopyroxene up to 20 μm in diameter. Plagioclase is abundant throughout the matrix as small turbid grains which display undulate extinction. Coarser (up to 500 μm) grains of plagioclase feldspar also occur in the matrix with some exhibiting albite twinning. Nickel-iron metal, troilite, chlorapatite and chromite occur as accessory minerals.

Microprobe analyses show that the olivine in the Chookkooning 001 meteorite is equilibrated with a

mean fayalite content of $\text{Fa}_{24.7}$ (range $\text{Fa}_{23.8-25.4}$, 30 analyses). The orthopyroxene shows only a small variation in chemical composition with a mean ferrosilite content of $\text{Fs}_{20.5}$ (30 analyses) and a wollastonite content of 1.5 mol%. Clinopyroxene was identified but the grains were too small to provide reliable analyses. The plagioclase content was found to be $\text{An}_{12}\text{Or}_{6.2}\text{Ab}_{81.8}$ (11 analyses).

The pyroxene geothermometers of Wells (1977) and Lindsley (1983) suggest that the Chookkooning 001 meteorite was heated to temperatures of between 700° and 800° C during metamorphism while the meteorite was still part of a large L type asteroid. The Chookkooning 001 meteorite is very similar in composition to the Mangalo meteorite, an L6, recently described from Eyre Peninsula (Wallace & Pring 1991).

CLASSIFICATION

The Chookkooning 001 meteorite has been classified as an L6 chondrite. The olivine composition is within the range of the L chondrites (Keil & Fredriksson 1964), and the orthopyroxene composition ($\text{Fs}_{20.5}$) shows that the meteorite

belongs to the olivine-hypersthene chondrite group. The highly equilibrated chemical composition, crystalline matrix, poorly defined chondrule boundaries, well recrystallized plagioclase and euhedral chlorapatite crystals suggest that Chookooning 001 belongs to the type 6 classification of Van Schmus & Wood (1967). The wollastonite content in the orthopyroxene is similar to that found in most L6 chondrites (Scott *et al.* 1986). The presence and content of plagioclase, the degree of crystal fracture and the undulate and mosaic extinction with planar fractures all indicate that the meteorite has been moderately shocked after metamorphism. According to the classification

scheme of Stöffler *et al.* (1991) the shock facies is estimated to be S3–4, moderately shocked.

ACKNOWLEDGMENTS

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**OBITUARY : SHANE ALWYN PARKER 3 AUGUST 1943 – 21 NOVEMBER
1992**

W. ZEIDELER

Summary

This obituary gives emphasis to Shane's work in marine invertebrates and lists all of his publications. His ornithological work was emphasised by Horton (1993).

OBITUARY

SHANE ALWYNE PARKER

3 August 1943 – 21 November 1992



This obituary gives emphasis to Shane's work in marine invertebrates and lists all his publications. His ornithological work was emphasised by Horton (1993).

Shane Alwyne Parker was born in Colchester, Essex where he attended schools gaining his O-Level in seven subjects. His interest in natural history developed early with walks in the English countryside with his aunt. He was an obsessive collector with an inquiring mind and often visited the Colchester Museum to identify natural history specimens that he had collected. Sadly, Shane's father did not approve of this "obscure" interest and, as Shane related to me, his life at home was not a happy one. At the age of 16 he began work at the British Museum, at Bloomsbury, initially as assistant in the Photographic Section, Reading and Map Room and later as assistant in the Bird Section of the Natural History Museum. He used to travel on the train from Colchester to London and back every day, leaving home at some ungodly hour each morning. Sometime later he moved to London and lived in a hostel where he obviously had a very merry time. He spent six and a half years at the British Museum, three as curator of their egg collection. In 1964 he took part in the second of the Harold Hall (British Museum) expeditions in Australia to northern Queensland from February to August. Those seven months were a highlight in Shane's life and influenced him to emigrate to Australia in 1967.

From 1967 to 1971 Shane worked for the Arid Zone Research Institute, Alice Springs, first as assistant to the Biologist and then to the Botanist, taking part in faunal and floral surveys of the Northern Territory and curating zoological and botanical collections. During this period (January – March, 1968) Shane undertook a solo trip to Choiseul and Malaita, Solomon Islands, in search of a species of ground-pigeon, without success (40). Later, working on a wallaby survey (39), he moved to Darwin where he met his future wife, Erica, whom he married in 1970 in Alice Springs. They moved to Adelaide in 1971 where Shane, feeling the need for a formal education, studied full-time at Daws Road High School to gain his Matriculation in 1972. He went on to complete a Bachelor of Science degree, majoring in Botany and Zoology, at the University of Adelaide in 1975.

During all this time Shane's lack of formal qualifications did not prevent him from publishing his observations. He published his first paper at the age of 16 (1) and by the end of 1967, while at the British Museum, had published 24 notes and articles, probably embarrassing some of his colleagues who encouraged him to emigrate. During his early years in Australia he continued to publish ornithological observations, corresponding regularly with other workers in Australia and overseas and while in Adelaide became an Honorary Research Worker at the South Australian Museum. When Herbert Condon retired as Curator of Birds in late

1974 Shane, while completing his final year at University, was asked to run the Bird Section until a replacement could be found. By this time Shane had published a further 25 articles including one on plants (38) and two on mammals (39, 47), the latter publication being a significant contribution. Logically and fittingly Shane was appointed Curator of Birds in January 1976 – a position which he held full-time until 1985 when he began his work as Curator of Lower Marine Invertebrates. This dual role continued until October 1991 although his work in ornithology consisted mainly of completing small research projects and training Dr Philippa Horton to take over the management of the Bird Section, the position of 'Curator of Birds' having been abolished. Tragically, by this time, Shane had been diagnosed with a lymphoma and although initial treatment seemed successful he lost his fight of about two years and died peacefully at home on 21 November 1992.

During his relatively brief lifetime Shane published some 118 notes and articles (including seven book reviews), more than 100 of them on ornithology. There is no doubt that Shane's knowledge of birds of the world and the Australasian bird fauna in particular was highly regarded worldwide, and it was for this reason that he was chosen as one of only five Australian delegates to visit China in 1981 under the auspices of the Australian and Chinese Museums Association (83). He was an active member of the South Australian Ornithological Association serving as Vice President in 1979–81 and 1985–86. He also served the Royal Australian Ornithologists Union as Councillor (1978–81), Chairman, Record Appraisal Committee (1979–82) and on the Taxonomic Advisory Committee (1979–83); and in 1978–81 he was on the Conservation Programme Committee of the World Wildlife Fund (Australia). He was also Secretary for the Royal Society of South Australia for the year 1986–87.

Amongst ornithologists Shane will best be remembered for his contribution to the Museum's bird collections. With the help of a dedicated band of volunteers, which he cultivated, Shane began the process of modernising the collection. Almost from scratch he began to establish parallel collections of skeletons, whole spirit specimens, nests and stomach contents. He conducted field work mainly to collect downy young and immatures of non-passerines, domestic species and neglected common species, and further augmented the collection and filled in gaps by exchanges with other museums. As a result of those activities the bird collections increased dramatically in size and scientific significance. In a relatively short time Shane, with his acquisition program and meticulous documentation, had transformed the Museum's bird

collections from one used mainly by bird watchers to one of science. He was always generous with his time making himself and the collection very available to bird enthusiasts and spent many hours encouraging young people to develop their interest in and knowledge of birds. Many of these people are now employed in the field of natural science and environmental studies. A highlight of his curatorship was the good relationship which he cultivated with the descendants of Captain S. A. White resulting in the donation to the Museum of White's African bird skin collections in 1976 and the main skin and egg collection in 1988. Shane's relationship with the White family culminated in the Museum's exhibition 'Captain White and the House of Birds'. Regrettably he died only 24 days before the exhibition opened.

Shane delighted in detective work, whether it was unravelling details of historical collecting expeditions and collections (18, 71, 91, 92, 108) or taxonomic problems (42, 88, 90). He also loved searching for 'lost' species (40, 62) and in 1979 joined an expedition on camel to search for the night parrot around Cooper's Creek. He believed as the only known specimens were discovered on camel he was more likely to succeed by these means if the bird was still extant. The party sighted four birds east of Lake Perigundi but Shane was not entirely convinced and never published a detailed account of the observations.

For his ornithological work Shane was honoured by the naming of a new subspecies of Honeyeater, *Acanthogenys rufogularis parkeri* (Parkes 1980) and two species of feather louse from the mallee fowl (Price & Emerson 1984; Emerson & Price 1986). On the latter Shane remarked "to the delight of my friends and the even greater delight of my enemies!". Although his career in Marine Invertebrates was brief he touched many with his enthusiasm, clarity of thought and meticulous research and his memory will be honoured by the naming of several species by various colleagues in future publications.

During the early 1980s Shane had some unfortunate disagreements with a few amateur ornithologists and his over-sensitive nature led him into deeper conflicts than need have been. These arguments came to a head over the description of a new sandpiper (79) resulting in a prolonged conflict and threatened legal action by both parties. These events were particularly distressing for Shane as he prided himself on his honesty and integrity and it hurt him deeply when he did not receive the support from his colleagues that he might have expected. In addition Shane was facing ill-informed criticism from a few amateur ornithologists and the public for the collection of specimens, particularly in regard to the Eyrean grasswren. Shane ultimately became very

disillusioned with the Australian ornithological community and in 1985 he switched his energies to the much neglected lower marine invertebrates.

Observing Shane working in the Marine Invertebrates Section was like watching a child with new found toys. There were just so many areas where he could apply his love for classical taxonomy. To his surprise and delight he found that new species could be found almost on a daily basis and new genera and families lurked in the collection or amongst newly acquired material from deep-sea trawlers.

Confronted with an array of animal groups, some of which he didn't even realise existed, he quickly sought out experts and corresponded with them. Much to his surprise he found them only too willing to help and share information. He corresponded often and developed a relationship with some colleagues that resulted in several joint publications describing the fauna of southern Australia. One of his major articles, and one of which he was justifiably proud, was a monograph on the stony corals of South Australia, Victoria and Tasmania which he produced with S. D. Cairns of the Smithsonian Institution as senior author (111). It was his last paper to be published before his death. Shane also published on polychaetes and bryozoans and at the time of his death was working on a couple of papers on leeches.

I was continually amazed by Shane's ability to comprehend the complex systematics of some phyla, if only to come up with a scheme of classification so that he could properly curate the collections. He very quickly identified specimens as best he could, completely reorganised the collections and curated them according to the most modern, acceptable classification. Whenever he came across a group for which he could not find an acceptable scheme of classification, he would write to one of the experts, usually overseas, and ask for help. Often this kind of correspondence led to the material being loaned for study, resulting in publications describing the unique fauna of southern Australia. Shane encouraged the use of the collections by others and was very generous with his time, often humbly accepting junior authorship for his efforts. He organised many exchanges of specimens and added substantially to the literature base of the collections. Shane was rewarded for his curatorial efforts when an overseas colleague, in a submission to the *Museum Review* 1991/92, remarked 'I have worked extensively at the U.S. National Museum, Smithsonian Institution and also at the British Museum and the collections at the South Australian Museum are far superior in quality'. These remarks and ones in a similar vein from other colleagues pleased Shane very much.

Shane soon came to realise that he could not do

everything and I encouraged him to specialise in polychaetes or bryozoans. It was the latter group that eventually 'grabbed' him and he was continually amazed by the diversity and beauty of the little 'critters'. Shane was never anyone to do things by halves and even when he was ill he was working on his checklist of Australian bryozoans which was to form the basis for future major taxonomic revisions of the entire Australian fauna. Fortunately for bryozoan workers Shane's checklist will be completed by his colleague and collaborator, Dr Peter Haywood, University of Wales, Swansea. But sadly, a wealth of knowledge passed away with Shane and we will never know the greatness that he was sure to achieve.

To some people, particularly to those who did not know him well, Shane was an English eccentric born about a century too late. He was a great admirer of Conan Doyle's hero, Sherlock Holmes and in winter often wore a tailor-made Edwardian frock-coat and wing collars. Although Shane loved elegant and stylish clothes, particularly the Edwardian fashions, and may have admired the life style of Edwardian society, that did not necessarily make him old fashioned. He was quite up with modern technology and methods and was instrumental in the purchase of a Scanning Electron Microscope for the Museum and used the instrument regularly for his research. However, I think he may have been more comfortable with computers had they been steam driven. Shane was widely read especially in ancient history, natural history and exploration and had a broad and deep knowledge of a wide variety of subjects. He was skilled at languages, took lessons in Gaelic and taught himself Latin while commuting on the train so that he could read the classics in the original. He also enjoyed a good detective story and was partial to the obscure and bizarre with Dan Dare comics, Winnie the Pooh, Molesworth and 'William' books being some of his favourites. He was an acknowledged authority on bawdy English folksongs which he could sing well in the appropriate accent. His collection of songs is regarded by some as one of the best in the world, valued for its academic content as well as for the many rare and original versions. Shane also loved fine music whether it was classical or modern with Pachelbel's Canon in D being one of his favourites. He was a talented artist and purchased his first bird book with money from selling his bird paintings to relatives and friends. He was particularly good at caricature and comic strips which provided an outlet for his wonderful, unique sense of humour. He enjoyed working in his vegetable garden and amongst his many other interests was that of steam trains and collecting finely engraved stamps and cigarette cards.

Perhaps his greatest passion was that of good food and wine. He was sometimes 'caught' in his office devouring some great custard pie or cream bun. Yet these gastronomic excesses had little effect on his slight frame. In the Marine Invertebrates Section, cream buns or preferably, huge creamy cakes, were compulsory on birthdays and whenever a paper was published – we seemed to have rather a lot of those! Shane was a founding member and the driving force behind the Museum select dining club *De Gustibus* and was the editor of its occasional organ *The Gullet*. This gave him a wonderful opportunity to make use of his creative writing skills. He loved the English language and took great delight in using it. He spent hours over the articles and the presentation of *The Gullet* and kept copies of all the issues. Perhaps as a result of his trip to China in 1981, where he attended many banquets of duck's feet and other unmentionable or unidentifiable gastronomic delights, it was the charter of *De Gustibus* to dine out at unusual places and sample unusual dishes. The annual *De Gustibus* Christmas Luncheon was a grand affair. It was the duty of everyone attending to provide an exotic dish that they had prepared together with good wine and champagne. Shane would address the meeting apologising for the absence of our fictitious president Sir Gregory Parsloe-Parsloe K.B. (Shane's alter-ego) who was unable to attend because of some hilarious and often disgusting, gluttonous mishap. The whole proceedings were always accompanied by live chamber music with Pachelbel's Canon being played at the beginning and end. For me these annual events were some of the most memorable of my life and I am grateful to Shane for the experience. Members of *De Gustibus* will be pleased to learn that before his death Shane honoured Sir Gregory by the naming of an appropriately large bryozoan; let us hope it gets published before the editor finds out! I will miss his good humour and sharp wit and I will never forget his last words to me as he said with a mischievous smile and knowing glint in his eye 'See you anon old bean'.

To Shane's wife Erica and their sons Gathorne and Tolle we extend our heartfelt sympathy.

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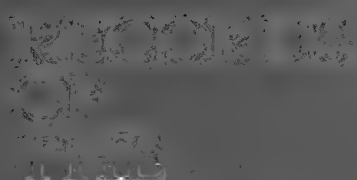
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RECORDS
OF
THE
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VOLUME 27 PART 2
OCTOBER 1994

**PROCEEDINGS OF THE FOURTH CONFERENCE ON AUSTRALASIAN
VERTEBRATE EVOLUTION, PALAEOLOGY AND SYSTEMATICS,
ADELAIDE, 19-21 APRIL 1994.**

INTRODUCTION

During the third Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, held in Alice Springs in 1991, delegates were asked to decide the venue of the next meetings two years thence. Rhys Walkley had reminded me that 1993 would be the centenary of the first expedition to Lake Callabonna. It therefore seemed fitting that Adelaide should host the 1993 meetings, and that in fact they should coincide with an exhibition about the Lake Callabonna fossils to be held at the South Australian Museum.

This offer was accepted, together with a non-exclusive theme of Plio-Pleistocene palaeontology, with Rod Wells (Flinders University of South Australia) and Neville Pledge (South Australian Museum) combining to organise the meetings and pre- and post-conference excursions. The organisers are grateful for the help given by Mr Gavin Prideaux in the program planning and printing of the abstracts.

The Conference was held in the Grosvenor Hotel, North Terrace, Adelaide, between 19-21 April 1993. More than fifty professionals, students and amateurs, several from overseas, attended to hear 49 papers read and to see eleven poster presentations. The student prize of an airline ticket to any Australian city for the purpose of study was donated by Australian Airlines. It was awarded to Ms Sanja Van Huet (Monash University) for her description of the Lancefield megafaunal site.

A five-day pre-conference excursion to Lake Callabonna and Lake Palankarina drew 13 participants, and an *ad-hoc* excursion to Naracoorte had 20 people.

During the Conference the exhibition 'Fossils of the Lake' was officially opened by Dr Richard Tedford (American Museum of Natural History), a veteran of two major expeditions to Lake Callabonna. The author is grateful to all who helped make the Conference a success.

NEVILLE PLEDGE

Curator of Fossils,
South Australian Museum

FOSSILS OF THE LAKE : A HISTORY OF THE LAKE CALLABONNA EXCAVATIONS

NEVILLE S. PLEDGE

Summary

The discovery of Diprotodon in Lake Mulligan in 1892 led to a major expedition by the South Australian Museum the following year. Initial reports indicated scores, if not hundreds, of skeletons exposed on the dry lake bed. Excavation showed the reality: most skeletons were incomplete and the bones badly badly eroded or rotten. Nevertheless, a large quantity of fossilised material was recovered, under trying circumstances, by the two-stage expedition, and returned to Adelaide. Preparation and repair of the bones took many years, and the first complete Diprotodon skeleton was unveiled in 1907. Other fossils includes a new species of giant bird, Genyornis newtoni, the giant wombat Phascolonus gigas (which proved the synonym of Scepharnondon) and several large extinct kangaroos.

FOSSILS OF THE LAKE: A HISTORY OF THE LAKE CALLABONNA EXCAVATIONS

NEVILLE S. PLEDGE

PLEDGE, N. S. 1994. Fossils of the Lake: a history of the Lake Callabonna excavations. *Rec. S. Aust. Mus* 27(2): 65–77.

The discovery of *Diprotodon* fossils in Lake Mulligan in 1892 led to a major expedition by the South Australian Museum the following year. Initial reports indicated scores, if not hundreds, of skeletons exposed on the dry lake bed. Excavation showed the reality: most skeletons were incomplete and the bones badly eroded or rotten. Nevertheless, a large quantity of fossilised material was recovered, under trying circumstances, by the two-stage expedition, and returned to Adelaide. Preparation and repair of the bones took many years, and the first complete *Diprotodon* skeleton was unveiled in 1907. Other fossils included a new species of giant bird, *Genyornis newtoni*, the giant wombat *Phascolonius gigas* (which proved the synonymy of *Sceparnodon*) and several large extinct kangaroos.

Subsequent expeditions by R. A. Stirton in 1953 and R. H. Tedford in 1970 have thrown more light on this, Australia's first Fossil Reserve, a 'veritable necropolis'.

N. S. Pledge, South Australian Museum, Adelaide, South Australia 5000. Manuscript received 1 February, 1994.

In 1831, while exploring the Wellington Valley of New South Wales, Major Thomas Mitchell found a fragment of a large jaw in one of the caves (Mitchell 1839). He sent it to Professor Richard Owen in London for identification. Owen, the world's leading anatomist of the day, soon realised that it came from a gigantic new species of marsupial, which he named *Diprotodon*, for its pair of large protruding incisor teeth ('two forward teeth') (Owen 1839).

Over the next few decades, Owen described more and more bones of the skeleton of *Diprotodon* sent to him by collectors in Australia, and eventually (Owen 1870, 1877), he published a skeletal reconstruction of the animal. But he was continually frustrated by the lack of associated footbones and he died in December 1892 without knowing their complex structure, only months before discoveries of complete skeletons would be made.

In 1870, a reward of £1 000 was offered for the discovery of a complete *Diprotodon* skeleton, and in the 1880s the discovery of skulls at Gawler (Howchin 1891) and Baldina Creek near Burra (Zietz 1890a), and associated bones at Bunday on the Murray Plains (Zietz 1890b), raised hopes that success would be attained. When word reached Adelaide in November 1892 that *Diprotodon* bones had been found on 'Mulligans Lake', north of Lake Frome, excitement swept the colony.

GEOMORPHOLOGY AND GEOLOGY

Originally called Lake Mulligan, Lake Callabonna is one of a chain of large dry salt pans (Fig. 1) that form a horseshoe around the northern Flinders Ranges from Lake Torrens to Lake Frome (Stirling 1894).

On the site of an ancient silted-up lake system (Callen & Tedford 1978), modern Lake Callabonna has been formed by deflation: the wind blowing dried salt, sand and clay particles to the east and north to form the Strzelecki Desert. In earlier times, the lake was considerably larger and intermittently full of fresh water (Tedford 1993). Stranded beaches may be found kilometres from the present shoreline.

During the Pleistocene, when the *Diprotodon*-bearing Millyera Formation was deposited, there was a fluctuating water level, as indicated by cyclic couplets of sand and laminated clay, the sand often being ripple-marked (shallow water or dry conditions) or desiccation cracked (dry/arid conditions). But the absence of fish fossils suggests the water in which the clay was deposited was too shallow or ephemeral to support them. Pieces of wood, and cones of the native pine *Callitris* indicate a wooded shoreline (Tedford 1973). Today it is virtually bare.

Later a more permanent lake formed supporting a plentiful fish and mollusc population. The



FIGURE 1. View of Lake Callabonna, looking south from the hill behind the 1893 camp. Photo: attrib. H. Hurst. SA Museum Heritage Collection.

mound springs then formed islands in the lake and were used as safe nesting areas for waterbirds whose bones have been found, and dated between 2 000 and 3 000 years old. This may still occur today, such as during the floods of the early 1970s when the lake was full for several years. There is evidence that Aborigines sometimes visited these islands in search of food such as swans' eggs, since worked quartzite flakes have been seen on one of them, associated with bird bones and eggshell fragments (pers. observ.).

HUMAN HISTORY OF THE AREA

Lake Callabonna falls within the sphere of the Pilatapa (Piladappa) Aborigines (Fig. 2) who occupied an area from Freeling Heights and Lake Frome to Lake Blanche and the southern part of the Strzelecki Desert, where an occupation site over 14 000 years old is known (Smith *et al.* 1991). Stone artefacts, including grinding stones possibly obtained from Prism Hill, south of Balcanoona, and polished stone axes (possibly traded from the east) have been found near the lake (pers. observ.). Ancient rock engravings are known in the Flinders Ranges. It is possible that the legendary 'Yamuti' (Tunbridge 1988) of the nearby Adnyamathanha people is a folk memory

of *Diprotodon* with which they could have been briefly contemporaneous, or at least a construction built on the knowledge of giant bones in the lake.

Robert Stukey named it Mullachon Lake in 1860, after the Aboriginal name for the mound springs on its western side. This soon became corrupted to Lake Mulligan.

The first European to see Lake Callabonna was Edward John Eyre in 1840. A few years later (1844), the lake was visited by Charles Sturt's party coming in from the east.

Pastoral activity started rather late, in the 1860s at Blanchewater. In 1882, John Ragless established his son Frederick B. (Fig. 3) on the Callabonna run, on the eastern side of the lake (Mincham 1967). In establishing the homestead (Fig. 4) Frederick Ragless found *Diprotodon* bones in a well nearby and these were sent to the South Australian Museum in 1885.

DISCOVERY

The Aborigines had long talked of large bones on the bed of Lake Mulligan, but they had been thought to be of bogged horses or cattle (Ragless 1893, *South Australian Register*, 7 July 1893). On 12 June, 1892 Ragless had accompanied an Aboriginal stockman to an area on the lake bed to

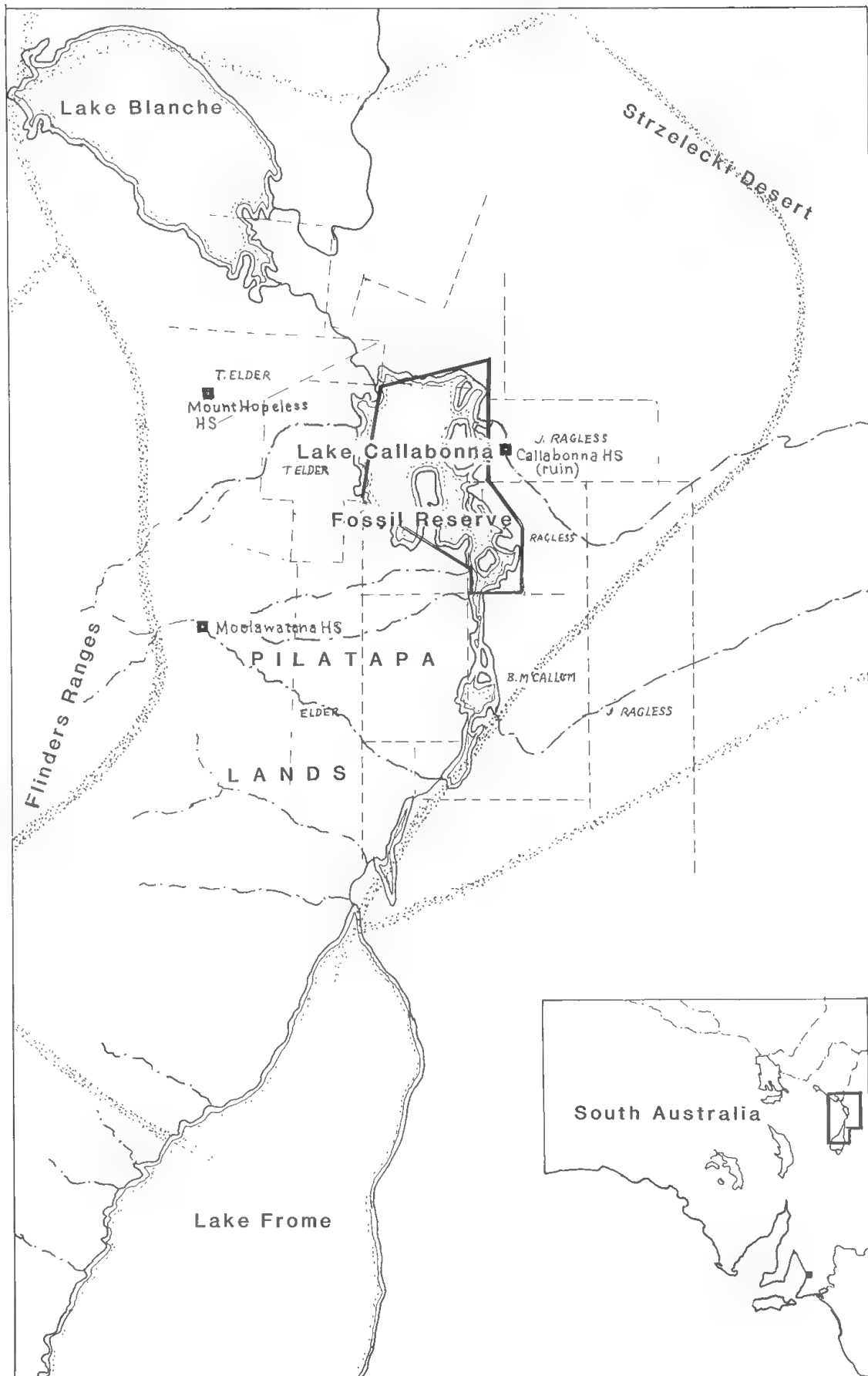


FIGURE 2. Map of Lake Callabonna and environs, showing the Pilatapa tribal area (after Tindale 1974) and some pastoral boundaries.



FIGURE 3. Frederick B. Ragless. Photo: courtesy L. Ragless.

see the bones (Fig. 5), following a conversation with the Aborigine a few days earlier when they had been talking about elephants. In his journal Ragless recorded that the boy, Jacky Nolan, had told him:

I bin tinkit elephant alonga this country one time. Me bin see'em bones. Me show'em you big fella bone alonga lake. 'Im much too big alonga panto [horse] (Ragless, unpubl.)

Ragless collected some of the bones and took them back to the homestead to show his men, and planned to take them to Adelaide at first opportunity. One of the men, John Meldrum, persuaded Nolan to take him back to the fossil site where he made his own collection. Shortly afterwards Meldrum 'left the station and came to town, where he exhibited the specimens at Mr P. Lee's Black Swan Hotel, North Terrace and claimed to be the discoverer' (*South Australian Register*, Thursday 6 July 1893, p. 4). Discovery of the bones led to a dispute over the reward which was never really settled.

Meldrum's arrival in Adelaide (*South Australian Register*, Tuesday 4 November 1892) with bones from Lake Callabonna was seized upon by the local press who followed succeeding events avidly. The *Register* (2 December 1892, p. 5) reported that the South Australian Museum was

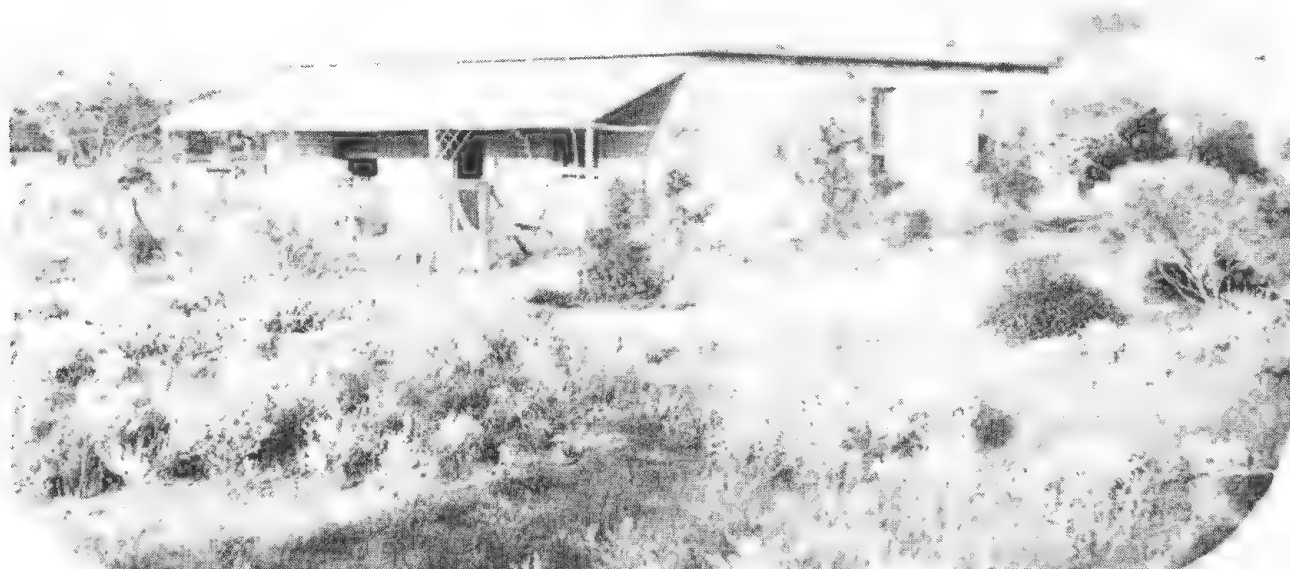


FIGURE 4. Callabonna Homestead, 1884. Photo: courtesy L. Ragless.

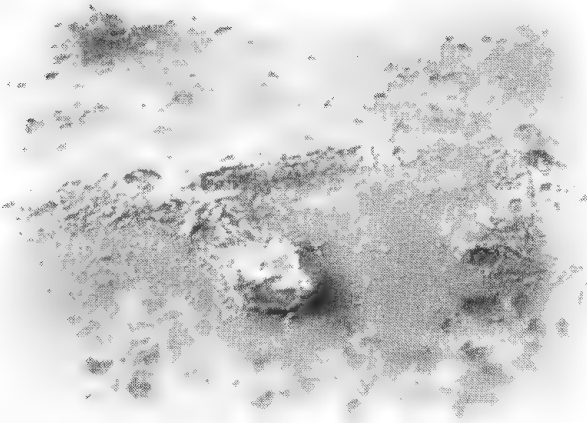


FIGURE 5. *Diprotodon* skeleton eroding out of the lake floor. Photo: attrib. H. Hurst. SA Museum Heritage Collection.

sending Henry Hurst to investigate the site. He left on 2 December 1892 and returned on 5 January with great news.

1893, Phase 1

Hurst's favourable report to the Museum Board was enough for them to send him back with a larger expedition and more detailed instructions.

Henry Hurst had worked for the Queensland

Geological Survey and had collected fossils of *Diprotodon* etc. from the black soils of the Darling Downs, so he seemed well suited to lead the expedition which left on 13 January for three months to conduct systematic searches and excavations for *Diprotodon* specimens. With him he took his brother George, John Meldrum, two labourers, and an Afghan to handle the camels and bring supplies. The party travelled by rail as far as Farina (409 miles/658 km), where they obtained camels and horse and buggy (Fig. 6) to go around the north end of the Flinders to Lake Mulligan/Callabonna. This last stage of 200 miles (320 km) took eight days to travel.

Hurst set up camp on an 'island' a couple kilometres from the edge of the lake bed, but after three weeks subject to the full force of the prevailing winds, moved it permanently to the western side of this island (Fig. 7). Excavations started at the spot first pointed out by Meldrum, but these specimens proved to be much decayed. Hurst used them, however, to instruct and train his inexperienced workers.

Hurst's reports to Stirling were initially sent every few weeks and were extravagant in their description of the deposit and his results. Later they dealt more with the problems encountered – irregular and late mails and shortage of feed and stores (Figs 8, 9) due to rains, requirements for



FIGURE 6. Hurst's party about to leave Bruce's Hotel, Farina, with camel team and buckboard, 1893. Photo: attrib. H. Hurst. SA Museum Heritage Collection.



FIGURE 7. Permanent camp, Lake Mulligan 1893. Photo: attrib. H. Hurst. SA Museum Heritage Collection.



FIGURES 8,9. All supplies were brought in by camel from many kilometres away. 8, water; 9, firewood. Photos: attrib. H. Hurst. SA Museum Heritage Collection.

sending the bones back to Adelaide and impending deadlines for the return of the camels and the cessation of the expedition. Hurst did, however, send accurate reports of new discoveries, such as the footpad impressions associated with the *Diprotodon* foot bones (letter, 16 March 1893), and the partial skeleton of a giant 'struthious' bird (letter, 6 May 1893), later to be named *Genyornis newtoni*. His excitement about the latter was such that he telegraphed the news of its discovery to Stirling. There was also a fossilised fruit, found near the bird remains, which he sent to Adelaide for identification. According to Hurst, Professor Ralph Tate (Adelaide University), identified it as *Frenela* (letter from Hurst, 20 June 1893), the old name for *Callitris* referred to by Stirling (1900).

Hurst suggested that he collaborate with Stirling in describing the *Diprotodon* remains, took a number of photographs of the operations (Figs 10, 11) and invited Stirling to see the site for himself. Occasional rain showers impeded work but by 25 May when the Government Geologist, H. Y. L. Brown, visited the site, 'three nearly complete skeletons of the diprotodon... [had] been unearthed (Fig. 12), together with over 2000 separate bones of the same animal belonging to over seventy individuals' (*South Australian Register* 23 May, 1893, p. 5). Stirling conveyed this information to



FIGURE 10. Excavating. The posted sign registers the area as a mining 'claim', but the details are illegible. The men are not identified but could include Meldrum. Photo: attrib. H. Hurst, SA Museum Heritage Collection.

the scientific world in a letter published in *The Times* (28 April 1893).

Brown's report (*South Australian Register*, 1 July 1893, p. 6; 1894) generally supported Hurst's claims of the fossil deposit. He noted that articulated footbones, encased in limy concretions that preserved apparent impressions of the sole of the foot, had been found. He further noted that bones of a giant wombat, kangaroos and a gigantic bird occurred in the deposit and he concluded by recommending 'that the whole area of the lake be reserved' for future scientific exploration, 'to prevent the indiscriminate digging up and removal of portions of the specimens.' This sentiment was heartily endorsed by the *South Australian Register* (31 July 1893, p. 6).

When heavy rain came in July, Hurst and Meldrum returned to Adelaide with some of the many bones they had excavated, leaving the rest of the party to continue work. Hurst's verbal report to the Museum Committee members enthused them enough to appropriate another £100 to cover his expenses. In addition two drays were to be despatched from Hawker to bring all the remaining bones from Lake Callabonna at an

estimated cost of a further £100. Hurst was to return to the lake forthwith to supervise this packing and dispatch, and await further instructions.

While in Adelaide, Hurst completed (29 July 1893) a preliminary report to the Museum Committee on his journey, excavations and geological observations. This formed the basis for Stirling's subsequent articles (Stirling 1900). Hurst also received a letter from his brother George, still at Lake Callabonna, reporting excitedly:

As soon as I had dug under the pelvis and into the exact spot where the pouch would be, I came on a dear little diprotodon humerus about six inches long. It is evident the large animal is a female and had a piccaninny diprotodon in her pouch when she died... The claim is very wet and the bones are very difficult to remove but you can depend I will get them all as I think this is the most wonderful discovery ever made in the world. (George Hurst July 1893, *vide* Tedford 1973).

This discovery exemplifies a problem that was beginning to emerge, for while some of these neonate bones have survived, they were, either at



FIGURE 11. Detail of the specimen in Fig. 10. Photo: attrib. H. Hurst. SA Museum Heritage Collection.

the time of excavation or subsequently in Adelaide, separated from those of the putative mother. Stirling was apparently already having misgivings about the procedures being used by Hurst, who had been concentrating on collecting bones that until then were unrepresented or poorly known in collections, and only rarely keeping associated bones together. Had the bones of mother and baby been kept together, the confusion over whether the two forms at Lake Callabonna were different sexes or different species (e.g. Williams 1982: Appendix IV) might have been resolved before now.

Stirling and his assistant, A. H. C. Zietz (Figs 13, 14), spent considerable time sorting through the bones brought down by Hurst, arranging them anatomically. Many had never been seen in such perfect condition, and those of the feet, tail and pouch (epipubes) had not been seen before (*South Australian Register* 31 July 1893, p. 6). Many had suffered during their journey to Adelaide because of poor packing though, and there was additional disappointment that no complete skeleton had been collected.

Stirling hoped that three or four complete

skeletons would be sent down to Adelaide in time to be exhibited at the September meeting of the Australasian Science Association (*South Australian Register* 1 August 1893, p. 5).

Hurst went back to the lake early in August, and was followed on 11 August by Stirling, Zietz and Thomas Cornock, the Museum's taxidermist and articulator.

1893, Phase 2

After inspection of the camp and excavation site, Stirling 'was very seriously dissatisfied with the way in which the work had been and was being carried on, [and] gave Mr Hurst and his brother a week's notice of the termination of their engagement, on which they with his consent, left at once.' The other men stayed on. It rained during Stirling's stay and he was unable to carry out the exploration he had hoped to do. After reorganising the party, he put Zietz in charge, confident of the work being done satisfactorily, and left for Adelaide on 21 August (Minutes, special committee meeting 31 August 1893).

Thomas Cornock, who had accompanied



FIGURE 12. Partially excavated *Diprotodon* skeleton. This specimen is lying on its belly, head to the right. Photo: attrib. H. Hurst. SA Museum Heritage Collection.

Stirling and Governor Kintore to Darwin (Palmerston) in 1891, made a number of pencil sketches of specimens and the excavations, which have only recently been rediscovered.

Following Hurst's departure and Zietz's assumption of control of the excavations, there seems to have been little news from the field until Zietz's return and his interview by a reporter from the *Adelaide Observer* (9 December, 1893, p. 33). Hurst had filled twenty-eight wooden cases with bones. Zietz added nearly sixty more. There was one complete skeleton of *Diprotodon*, in good condition, another not so good, and a third of possibly another, smaller species. Amongst other things, they had collected one skull of the giant bird and fragments of another one, a skeleton of the giant wombat and two skeletons of extinct kangaroos, as well as a second juvenile *Diprotodon* (Fig. 15).

Weather and working conditions deteriorated as the year wore on. The drought worsened, as did the rabbit plague. Constant dust storms caused 'sandy blight' eye problems, and the dying rabbits and bad water contributed to gastric illness. Finally heavy rains in November made excavation

impossible and the party returned to Adelaide amid great interest from the public and praise from Stirling.

The expedition had originally been financed by the Museum – £250 being scraped from their meagre budget for three months work. This soon ran out and the operation was saved by a generous gift of £500 from Sir Thomas Elder. The Museum was also indebted to the Surveyor General, Mr G. W. Goyder and Mr Peter Waite for services such as supplying camels. Mr Frederick Ragless assisted in various practical ways. Ragless and Meldrum both applied for the reward for the discovery of the *Diprotodon* skeletons. The Museum Board rejected Meldrum's claim in favour of Ragless, but because of the huge financial costs engendered by the expeditions, they were unable to pay the reward.

THE SPECIMENS

Despite the various problems encountered by the 1893 expeditions, a large number of bones were collected. By far the most numerous were the



FIGURE 13. Dr Edward C. Stirling. Photo: SAM Photo Library.



FIGURE 14. A. H. C. Zietz. Photo: SAM Photo Library.

remains of *Diprotodon* – some eighty specimens were investigated and at least partially collected. Also collected were partial skeletons of several giant birds (*Genyornis*), two giant wombats (*Phascolonius*) and some kangaroos (*Sthenurus* and *Macropus*), as well as the fragmented impressions of *Diprotodon* foot pads, and a mass of comminuted twigs found in the gut region of a *Diprotodon* (Stirling & Zietz 1899).

Reading through Hurst's letters, it is apparent that the list should be larger than this. For instance, he mentions (20 June 1893) several skeletons of a new wombat just found by his brother, that may have 'exceeded a bullock in size', and 'a minute mammal which must prove new to science. The tibia of the latter measures about 2½ inches [6.3 cm] in length'. Although Hurst intended bringing the latter with him to Adelaide, Stirling apparently never saw it and its whereabouts (and identity) is unknown.

CREATION OF THE FOSSIL RESERVE

The South Australian Government Geologist H. Y. L. Brown visited Lake Callabonna in June

1893. At the end of his report (1894) he recommended that the lake bed be proclaimed a Fossil Reserve 'to prevent the indiscriminate digging up and removal of portions of the specimens' (the suggestion came at a time when an Adelaide syndicate was being floated to do just that).

Brown's far-sighted suggestion was duly followed, and on 5 December 1901 the Lake Callabonna Fossil Reserve was gazetted. It is believed to be the first fossil locality in Australia, and one of the first in the world, to be so declared.

AFTERMATH

Following his return to Adelaide with the bulk of the fossils found at Lake Callabonna, Zietz immediately plunged into the task of sorting and repairing bones, and compiling a composite set from which to cast a complete skeleton (Stirling 1907). This took many years. The problem was that the bone was impregnated with salts, mainly sodium sulphate, which soaked up moisture during winter and made cleaning and restoration, with the facilities, methods and materials then

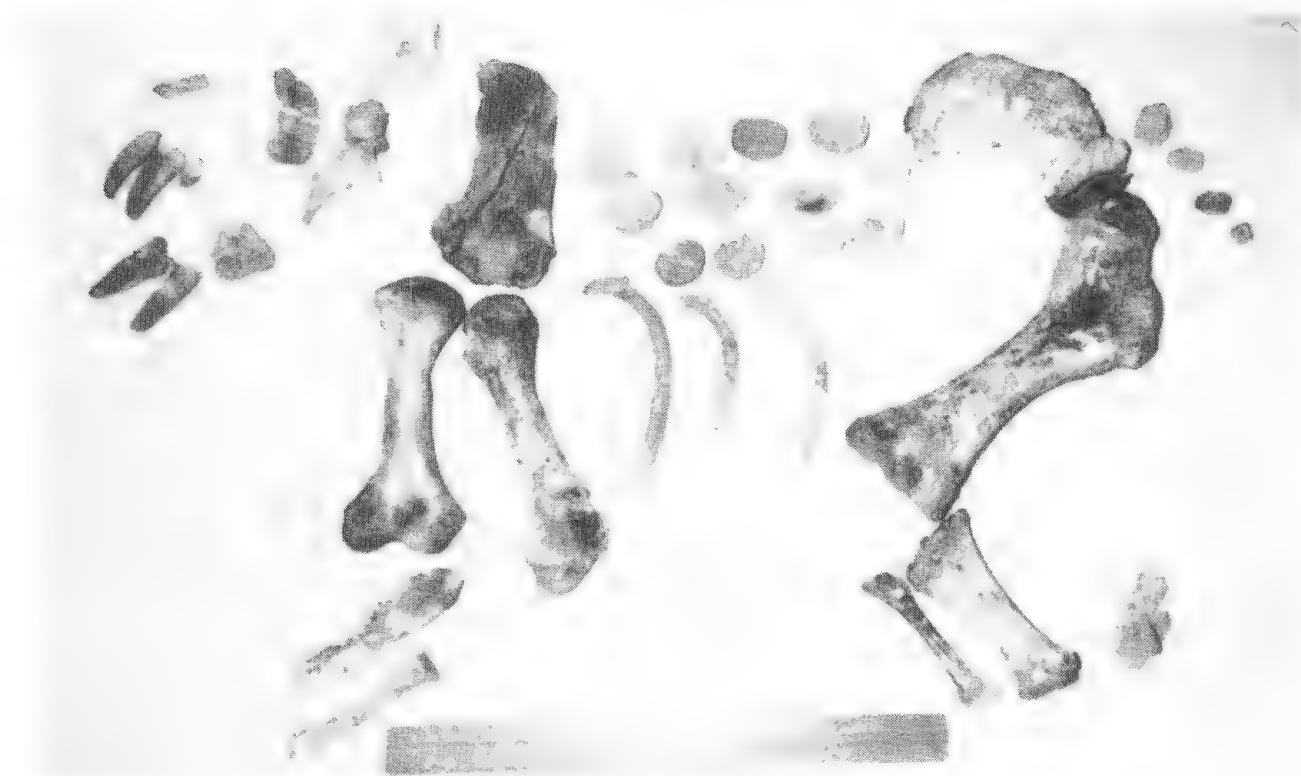


FIGURE 15. Associated bones of the juvenile *Diprotodon* found by Zietz's party, August 1893. SAM P10563 Photo: N. Pledge.

available, very difficult (Hale 1956). Meanwhile, he assisted Stirling in describing the giant bird *Genyornis*, and the feet of *Diprotodon* (Stirling & Zietz 1896, 1899a,b). Casting of the bones was done by Robert Limb, father of the entertainer of the same name. A restoration painting of *Diprotodon* in life was done by C. H. Angas (Stirling 1907).

For his part, Stirling decided in 1894 that the lake should be called Lake Callabonna (Board Minutes, 2 February 1894) after Ragless' sheep run that bordered it on the east. It had never formally been named – its common name, Lake Mulligan, was a corruption of 'Mullachon', the name given it in 1860 by Robert Stukey. This was the Aboriginal name for the mound springs on the western side that still are known as Mulligan Springs.

Stirling's study of the fossil remains resulted in several short articles (1893a,b, 1894a,b, 1896a,b, 1900, 1907), and a series of six monographs published in the specially created *Memoirs of the Royal Society of South Australia* between 1899 and 1913.

While Zietz was working on the skeleton of *Diprotodon*, Stirling travelled overseas, visiting museums. Several were interested in obtaining a cast or duplicate specimens of bones of

Diprotodon, and in this way he obtained by exchange the dinosaur *Diplodocus* leg bones on display on Level 1 of the South Australian Museum. Seven casts of the *Diprotodon* skeleton were eventually distributed.

Preparation of the *Diprotodon* cast was completed in 1906 and unveiled to the public in 1907, together with numerous other specimens.

CONCLUSIONS

After 1893, Lake Callabonna lay almost forgotten and undisturbed by scientists for sixty years. The only known visits were by Robert Bedford, of the privately-owned Kyancutta Museum, in 1928 (Cooper 1987) and H.O. Fletcher (1948) from the Australian Museum. It is not known what Bedford collected, but Fletcher found nothing, apparently having gone to a different part of the lake, away from the 1893 site.

In 1953 the Board of the South Australian Museum, at the urging of new member C. W. Bonython, suggested to University of California researcher Professor R. A. Stirton, visiting Australia in search of Tertiary mammals, that reinvestigation of Lake Callabonna would at least bring some positive results for his expedition.

Stirton and Fulbright student R. H. Tedford, together with Museum and University of Adelaide personnel (Stirton 1954) spent three weeks excavating near the site of the 1893 camp which they were able to relocate. Several specimens of *Diprotodon* were collected and taken back to the University of California Museum of Paleontology at Berkeley to be prepared and ultimately studied.

Tedford became fascinated by the locality and in 1970 led a joint expedition with the Smithsonian Institution and South Australian Museum, with excellent results (Tedford 1973). Although *Diprotodon* was the first objective, more important specimens were of *Genyornis* (e.g. Rich 1979), *Phascolonius*, *Protomnodon* and *Sthenurus* (Wells and Tedford in prep.). In 1983 T. Rich and P. V. Rich, with logistic support from the Australian Army, returned to search (fruitlessly) for more *Genyornis* material.

Stirton's 1953 trip could be said to be the beginning of modern mammalian palaeontology in Australia, since it stirred academic and public interest and spawned a growing number of

Australian and American students with an interest in the Tertiary and Quaternary of this continent.

We must not, however, forget the thoughtful and interested pastoralists such as Frederick Ragless and enthusiasts like Henry Hurst, and explorers such as Thomas Mitchell who initially brought these fascinating fossils to scientific and public notice.

ACKNOWLEDGMENTS

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SUCCESSION OF PLIOCENE THROUGH MEDIAL PLEISTOCENE MAMMAL FAUNAS OF SOUTHEASTERN AUSTRALIA

RICHARD H. TEDFORD

Summary

Southeastern Australia contains the most completely documented Pliocene-Pleistocene faunal succession known on the continent. Magnetostratigraphic, geochronologic and palaeontologic data from the Murray and coastal Victorian basins provide a chronology for local faunas covering early Pliocene through medial Pleistocene time. Changes in the composition of these assemblages appear to be congruent with the physical and palaeobotanical history of southeastern Australia.

SUCCESSION OF PLIOCENE THROUGH MEDIAL PLEISTOCENE MAMMAL FAUNAS OF SOUTHEASTERN AUSTRALIA

RICHARD H. TEDFORD

TEDFORD, R. H. 1994. Succession of Pliocene through Medial Pleistocene mammal faunas of Southeastern Australia. *Rec. S. Aust. Mus.* 27(2): 79–93.

Southeastern Australia contains the most completely documented Pliocene–Pleistocene faunal succession known on the continent. Magnetostratigraphic, geochronologic and palaeontologic data from the Murray and coastal Victorian basins provide a chronology for local faunas covering early Pliocene through medial Pleistocene time. Changes in the composition of these assemblages appear to be congruent with the physical and palaeobotanical history of southeastern Australia.

The early Pliocene marine transgression in the Murray and coastal basins was accompanied by the spread of rainforest containing diverse arboreal mammals and genera now restricted to the tropics. At the generic level early Pliocene assemblages resemble later faunas and include the earliest appearance of some living and Pleistocene genera along with genera known only from the early Pliocene. Marine regression in the medial Pliocene restored more continental climates to southeastern Australia but the presence of a large lake in the Murray Basin sustained wet sclerophyll vegetation. Living genera whose species now occupy inland environments began to appear there.

At the close of the Pliocene and beginning of the Pleistocene, forms close to living species appear as do species of extinct genera that became common elements in medial and late Pleistocene faunas. Wet sclerophyll vegetation was restricted to the highlands and drier shrubland associations developed in the lowlands as the temperate latitudes of Australia responded to global climatic cooling. By the time more rapid cycling of world climate appears in the medial Pleistocene, the southeastern Australian fauna included most of the associations of taxa that characterized the later part of the Quaternary.

Richard H. Tedford, American Museum of Natural History, New York, N. Y. 10024.
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Data reviewed by Woodburne *et al.* (1985) on the succession of mammal faunas in the Murray and adjacent Otway and Gippsland basins of southeastern Australia suggested their singular potential in defining a Pliocene and Pleistocene biostratigraphy for that part of the Australian continent. The locations of most of these faunas are shown in Figure 1. Subsequent study of these assemblages, and further calibration of their succession using paleomagnetic methods (An *et al.* 1986; MacFadden *et al.* 1987; Whitelaw 1989, 1991, 1993) has made it possible to look in more detail at the temporal ranges of taxa and to correlate faunal change with physical and biotic events deduced from other data.

The purpose of this contribution is to examine the chronologic ranges of taxa, principally at the generic level, and then to consider the possible ecological factors that might have guided the succession based on genera whose living species have known habitat preferences. Such extrapolations must be tempered by evidence of

shifting habitat for some forms. The pygmy possum *Burramys* is a case in point in which the Pliocene species were associated with lowland rainforest yet its living species is an inhabitant of temperate alpine environments (Flannery *et al.* 1992). It is also important to remember that knowledge of the succession of local faunas and their contained taxa is limited by the geological record of southeastern Australia. Therefore the observed stratigraphic ranges in that area represent only parts of the total ranges of the taxa. Further perspective on the temporal ranges of some Pliocene taxa can be made by comparison with the Lake Eyre Basin and northern Queensland where similarly calibrated faunas are known.

As Whitelaw (1991) pointed out, the magnetostratigraphies relating to individual local faunas cannot in themselves be correlated with the Geomagnetic Polarity Time Scale without evidence from other geochronological disciplines. His work on the faunas of southeastern Australia emphasized those assemblages from deposits

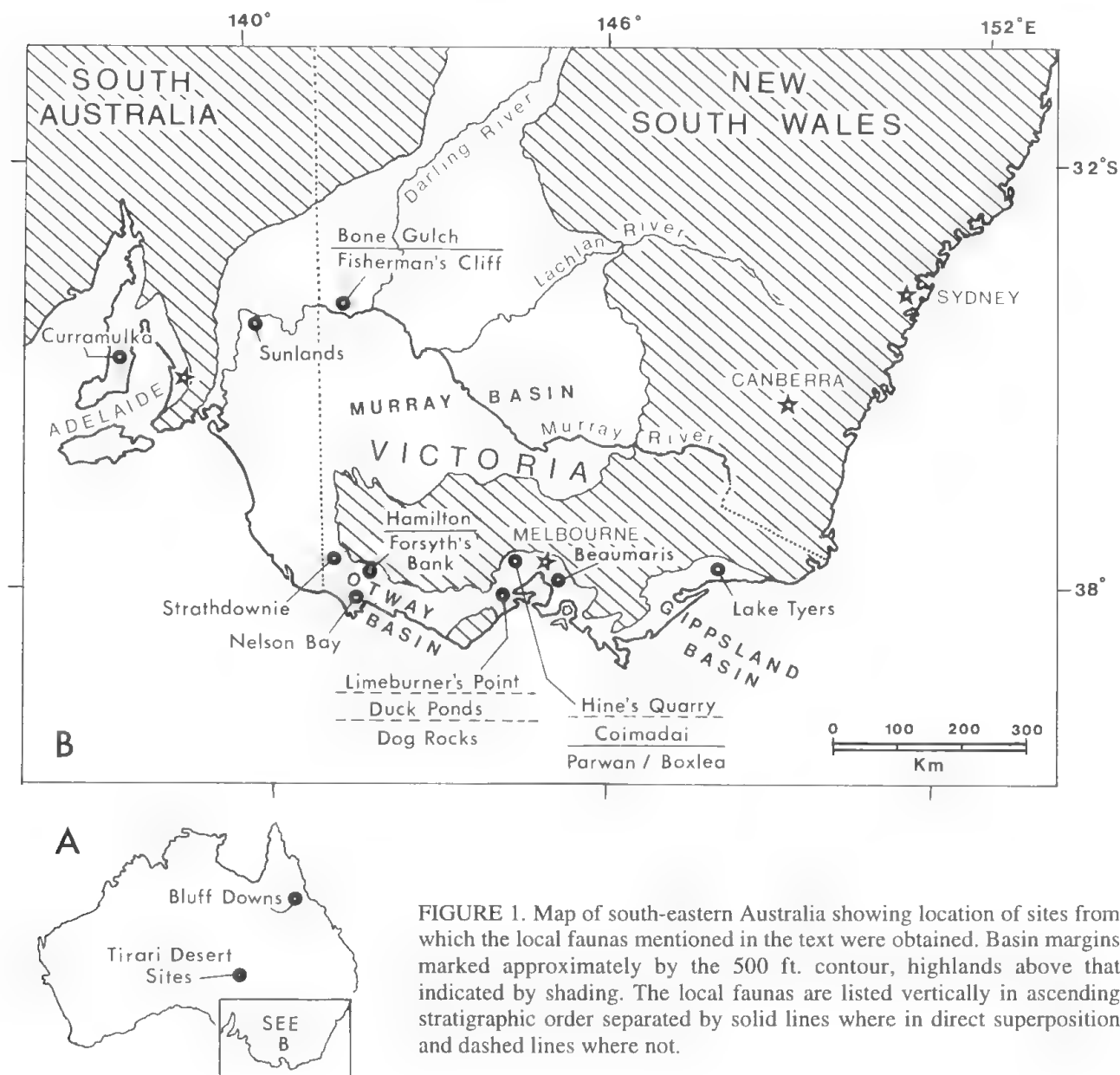


FIGURE 1. Map of south-eastern Australia showing location of sites from which the local faunas mentioned in the text were obtained. Basin margins marked approximately by the 500 ft. contour, highlands above that indicated by shading. The local faunas are listed vertically in ascending stratigraphic order separated by solid lines where in direct superposition and dashed lines where not.

interbedded with volcanic rocks that have been dated using radioisotopic methods. In the case of the Nelson Bay Local Fauna (MacFadden *et al.* 1987; Whitelaw 1991) the presence in the deposits of age-diagnostic planktonic foraminifera provided additional calibration. The Murray Basin sites lie within a longer magnetostratigraphic section that An *et al.* (1986), and Whitelaw (1991) correlate as lying within the Gauss through early Matuyama chrons using the pattern of polarity reversals. In any case, the chronological data constrain the fossil assemblages only to spans of time; shorter where the data are best, and longer where more loosely defined. The correlation chart (Fig. 2) shows these estimated ranges, and the range chart (Fig. 3) uses these estimates of maximum and minimum temporal range for taxa. In addition the

total known range is indicated both within and outside southeastern Australia.

This paper follows Cande and Kent (1992) in the calibration of epoch and informally designated subepoch boundaries: Miocene–Pliocene boundary, 5.3 Ma; early Pliocene–medial Pliocene boundary is the Gilbert–Gauss boundary, 3.55 Ma; medial Pliocene–late Pliocene boundary is the Gauss–Matuyama boundary, 2.60 Ma; Pliocene–Pleistocene boundary, is at the end of the Olduvai Subchron, Matuyama Chron 1.76 Ma; early Pleistocene–medial Pleistocene boundary is informally set at the end of the Matuyama Chron, 0.78 Ma; medial Pleistocene–late Pleistocene boundary is informally set at 0.40 Ma; late Pleistocene–Holocene boundary is at 0.01 Ma (Ma: million years on the geological time scale;

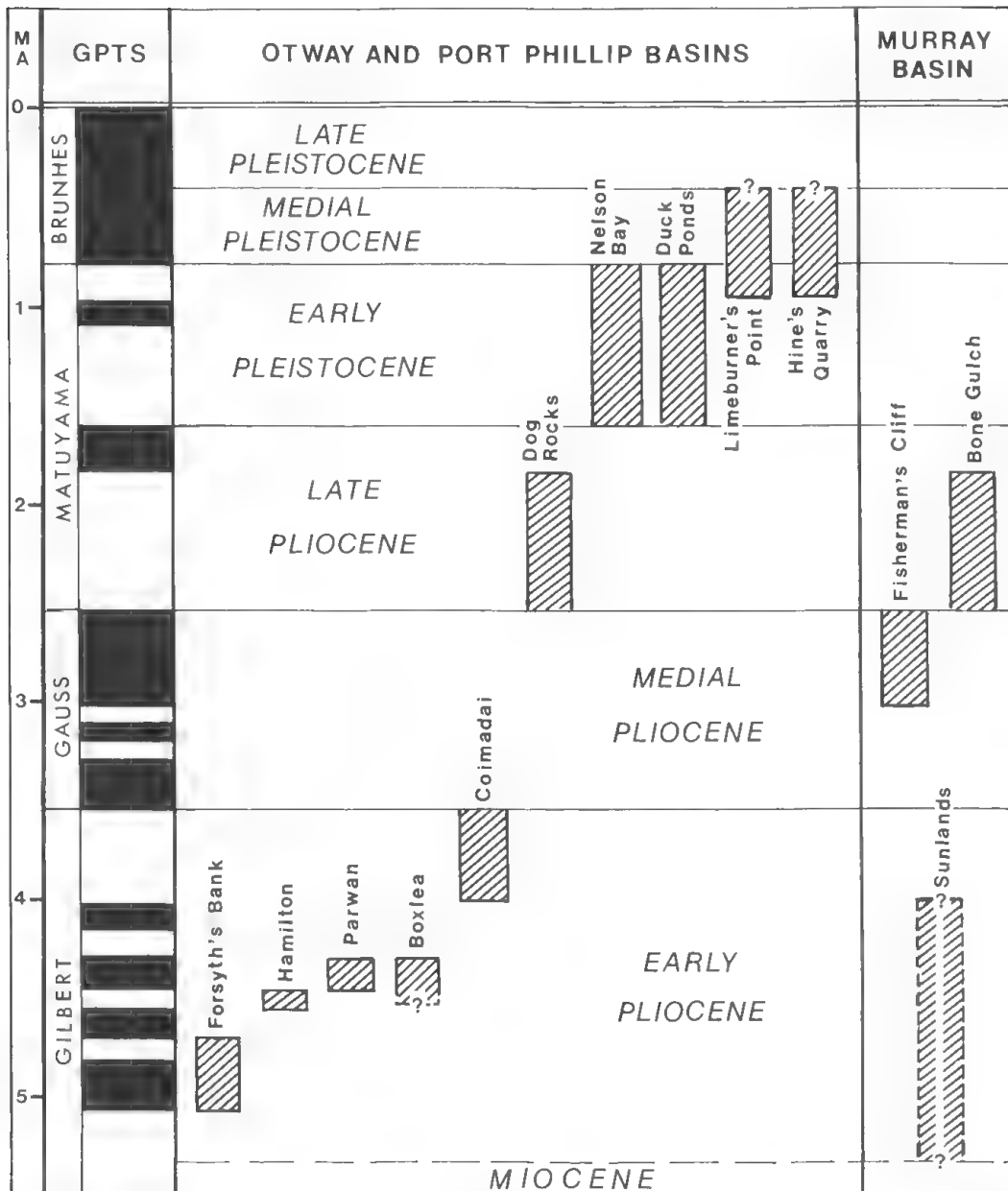


FIGURE 2. Approximate limits in time for the local faunas discussed in the text as deduced from palaeomagnetic data and correlations to the Geomagnetic Polarity Time Scale (GPTS). Although each local fauna is essentially a point in geologic time this cannot be more closely constrained than the limits shown (Whitelaw 1991). The Sunlands Local Fauna from the Murray Basin has no supporting paleomagnetic data, but is given a chronologic position correlative with assemblages in the Otway Basin that belong to the early phase of the Pliocene transgression recorded in both basins. Calibration of the GPTS follows Cande and Kent (1992).

M.y.: span of time, millions of years long).

Extinct taxa are indicated in the text by a preceding asterisk *.

THE FAUNAL RECORD

The geochronological range chart (Fig. 3) plots the time spans for selected genera of marsupials and one family of rodents. These are arranged to show the succession of forms, but the following

analysis of this record will discuss each family in systematic order. The best available faunal lists are given by Rich *et al.* (1991) and the sources for these lists are given there. Since 1991, additional faunas, pertinent to this review, have appeared including those in Flannery *et al.* (1992); Pledge (1992); Tedford and Wells (1992) and Turnbull *et al.* (1992 and 1993). Whitelaw (1991, 1992) gives lists for the Pleistocene faunas and references. An asterisk indicates extinct taxa. Two sites deserve further discussion:

The newly described Curramulka Local Fauna (Pledge 1992) from Yorke Peninsula, South Australia (Fig. 1) appears on stage-in-evolution criteria of its marsupials to predate the assemblages discussed here. The fact that it contains several genera that are components of Pliocene and Pleistocene faunas of southeastern Australia suggests that the Curramulka Local Fauna is at least of late Miocene age. The local fauna contains a number of arboreal forms but lacks those having species in present-day rainforest. It provides valuable perspective in our assessment of the history of certain genera and relevant information from this fauna will be included in the following summaries and discussion.

The Beaumaris marsupial assemblage from the Port Phillip Basin (Fig. 1) consists of five specimens collected over the past one hundred years from outcrops of the Black Rock Sand Member of the Sandringham Formation at Beaumaris. Producing strata include the nodule bed that lies directly on a surface cut on the medial Miocene Fyansford Formation, and the overlying calcareous and ferruginous sands. None of the material has precise provenance, but differences in permineralization suggest different geochemical environments that may be indicative of stratigraphic position. In an effort to test the provenance of the material Gill (1957a) determined the flourine-phosphate ratios of the bony parts of three of the specimens and found a spread of values separated by only 0.5–0.6%. Similar determinations from the bony parts of shark teeth, some known to be from the “nodule bed,” produced a similar range of values. Gill concluded that the nodule bed was the probable source of the marsupial bones. Despite this there is still the possibility that the Beaumaris marsupial assemblage is a composite of older remanié and younger autochthonous material. Carter (1978) examined foraminifera from the “nodule bed” and found remanié material, the youngest of which was of medial Miocene age. Miocene squalodont whale teeth and the nautiloid **Aturia* from Beaumaris also suggest that they are remanié lying within the “nodule bed” on the surface of disconformity.

The heavily permineralized **Kolopsis* sp. right ramus (Nat. Mus. Vict. P15911) described by Stirton (1957) and Woodburne (1969 as *Zygomaturus gilli*) is water-rolled and bored from exposure on the marine platform developed on the Fyansford Formation. A left ramus of **Kolopsis* sp. (Nat. Mus. Vict. P16279), purchased by the

Museum of Victoria from Albin Bishop in 1910 and thought to be from Chinchilla, Queensland (Stirton 1957: 128), may actually be from Beaumaris because it is encrusted with calcareous tubes of spirorbid worms (T. Rich, pers. com. 1979) and preserved in a manner similar to NMV P15911. These specimens may be remanié. Murray *et al.* (1993) compare **Kolopsis* sp. with **K. yperus*, a taxon from Miocene deposits disconformably overlying those that contain the Alcoota Local Fauna in Northern Territory. They contend that **Kolopsis* sp. lies morphologically between **K. torus* (Alcoota) and **K. yperus*, thus supporting a Miocene age for **Kolopsis* sp. on stage-in-evolution criteria.

The **Zygomaturus gilli* holotype P3/ and referred maxilla (Stirton 1957) and more recently discovered lower molar (Rich 1976), are more pristine in preservation and may actually be derived from the immediately overlying Black Rock Sand. In their evaluation of zygomaturine phylogeny, Murray *et al.* (1993), place **Z. gilli* above **K. yperus* at the base of the genus **Zygomaturus* further emphasizing its phylogenetic separation from **Kolopsis* sp. Rich *et al.* (1991) add '*Palorchestes* sp.' to the Beaumaris faunal list, but this reference seems to come from older identifications of the **Z. gilli* holotype cited in the synonymy provided by Stirton (1957).

The marine invertebrate fauna of the transgressive Black Rock Sand was used by Singleton (1941) to typify his Cheltenhamian Stage. Despite the similarity of its molluscs to those of the succeeding Kalimnan stage, he assigned the Cheltenhamian to the Upper Miocene, largely on the basis of the occurrence of teeth of the cetacean *Parasqualodon* and the nautiloid *Aturia* not known to survive the Miocene, but very likely remanié at Beaumaris as stated above. Elsewhere in the Port Phillip and Gippsland basins a surface of disconformity of similar character, developed on Miocene marine strata, is overlain by marine deposits of Kalimnan age (including the deposits containing the type fauna defining the age at Lake Tyers, Gippsland). In Gippsland the Jemmys Point Formation also rests on the same phosphatic nodule-bearing surface of disconformity (Carter 1978). The evidence thus seems to indicate that molluscan faunas indicative of the Cheltenhamian and Kalimnan stages belong to the same transgressive interval. Furthermore Darragh (1985) showed that molluscan assemblages typical of the Cheltenhamian and Kalimnan are superposed

within the Jemmys Point Formation outcrops at Bunga Creek near Lakes Entrance, Victoria. Ludbrook (1973: 253–255) gave an historical review of this problem which has become entwined with efforts to recognize the Miocene–Pliocene boundary.

For the purposes of this review, a Pliocene age is assigned to the initiation of the Kalimnan transgression. The earliest molluscan faunas associated with this transgression are of Cheltenhamian composition. They are associated with terrestrial vertebrates only at Beaumaris. If **Zygomaturus gilli* is autochthonous in the Black Rock Sand, it represents the oldest Pliocene taxon in southeastern Australia. The marine Grange Burn Coquina, with an occurrence of the kangaroo **Kurrabi* sp. (Forsyth's Bank Local Fauna), contains a molluscan fauna of Kalimnan type (Ludbrook 1973) representing a later phase of the Pliocene transgression. This unit is not well constrained magnetically (Fig. 2 and Whitelaw 1991).

Dasyuridae

Most species are small so that the record of this group is biased toward those sites that have been screen-washed. Some living genera have Pliocene records: *Sminthopsis* sp. cf. *S. macroura* (Fisherman's Cliff), *Antechinus* sp. (Hamilton, Fisherman's Cliff, Dog Rocks), *Satanellus hallucatus* (Fisherman's Cliff), *Dasyurus* sp. (Fisherman's Cliff, Dog Rocks), and *Dasyuroides achilpata* (Fisherman's Cliff). The living *Sminthopsis crassicaudata* has a medial Pleistocene record at Hine's Quarry. The record of the largest dasyurid, *Sarcophilus*, begins in the early Pliocene with an unallocated species (Parwan) followed by a relatively primitive species, *S. *moornaensis* (Fisherman's Cliff), in the late Pliocene. Representatives of the living species, or its close ally *S. *laniarius* (a subspecies of *S. harrisii* to some, Werdelin 1987), occur in early Pleistocene deposits (Limeburner's Point). **Glaucodon ballaratensis*, which appears to be a member of the Tasmanian Devil clade, occurs only in deposits at Smeaton, Victoria, that have a Late Pliocene maximum age (Turnbull *et al.* 1993). This genus is thus overlapped in range by its sister taxon *Sarcophilus*.

Thylacinidae

Curiously, there is no Pliocene record of thylacines in southeastern Australia but the genus is recorded in the Miocene Curramulka Local Fauna of South Australia (Pledge 1992). There is

a long record of the genus extending from the Miocene into the late Pleistocene in northern Australia and New Guinea. The Nelson Bay species, close to the modern *Thylacinus cynocephalus*, may be the earliest known occurrence of this recently extinct taxon.

Peramelidae

This family is also poorly represented in the record, very likely because all members are small animals. Unidentified peramelids occur at Hamilton and Fisherman's Cliff, but at Dog Rocks, at the close of the Pliocene, *Perameles* sp. and *Isoodon* sp. are both recorded.

Thylacomyidae

There are no records of bilbies in southeastern Australia until the late Pleistocene when *Macrotis* is present in the Murray Basin.

Thylacoleonidae

Fragments of the dentition and skeleton of **Thylacoleo* sp. were recovered with the Curramulka Local Fauna (Pledge 1992) of South Australia. The nearby Town Cave produced a single P3/, the type of **T. hilli* Pledge 1977, which is the most primitive member of the genus and could be a contemporary of the Curramulka assemblage. Unfortunately the fragments from these sites do not include comparable elements, nevertheless the records do indicate the presence of the genus prior to its Pliocene appearance in southeastern Australia. This record begins with **Thylacoleo* sp. at the late Pliocene Bone Gulch site in the Murray Basin. Material that can be identified with the widespread Pleistocene species, **T. carnifex*, occurs in the early Pleistocene Duck Ponds Local Fauna.

Vombatidae

Pledge (1992) records *Vombatus*, *Phascolonus* and '*Phascolomys*' sp., cf. '*P.*' *medius* from the later Miocene Curramulka Local Fauna of coastal South Australia. Early Pliocene representatives of *Vombatus* are known at Boxlea and Coimadai, including *V. *parvus* as well as a larger form, *V.* sp. *Vombatus ursinus* is also present at Dog Rocks by the late Pliocene. *Lasiiorhinus* is present by medial Pliocene time in the Murray Basin (Fisherman's Cliff) and a large species, comparable to '*Phascolomys*' **medius*, is present in the Port Phillip Basin (Limeburner's Point) by the medial Pleistocene. Giant wombats also occur in the late Pliocene, **Phascolonus* sp. (Dog

Rocks) and **Ramsayia* sp. cf. *R. magna* (Bone Gulch).

Diprotodontidae

Remains of these large animals are present at nearly all sites providing a more continuous record than for other groups except the Macropodidae. There is considerable late Cainozoic diversity within the family, perhaps denoting a span of maximum cladogenesis within the group. The diprotodontid record in southeastern Australia in the Pliocene includes the diprotodontines **Euowenia* sp. (Coimadai), a new genus at Hamilton, and, perhaps, **Diprotodon* itself at Fisherman's Cliff and Dog Rocks. The earliest record of **Zygomaturus*, *Z. gilli*, occurs in the Black Rock Sand at Beaumaris in the Port Phillip Basin. This is here regarded as earliest Pliocene as discussed above. Other Pliocene occurrences of **Zygomaturus* sp. are known at Coimadai and Dog Rocks. **Zygomaturus trilobus* and **Diprotodon* sp. are present at Nelson Bay in the early Pleistocene. By medial Pleistocene time **Diprotodon optatum* is present at Duck Ponds (as '*D. longiceps*'), Limeburner's Point and Hine's Quarry. The continent-wide diprotodontid record shows a reduction in diversity at the close of the Pliocene with only **Diprotodon optatum* and **Zygomaturus trilobus* extending into the late Pleistocene.

Palorchestidae

A relatively primitive early Pliocene species, of **Palorchestes*, perhaps close to the northern Australian Miocene *P. painei*, occurs at Hamilton. A similar form occurs in the later Miocene Curramulka Local Fauna of South Australia (Pledge 1992). The small **P. parvus* is present in the early Pleistocene (Nelson Bay) and this taxon survives into the late Pleistocene at Strathdownie Cave in western Victoria (Gill 1957b). There is no early record of the giant **P. azael* in southeastern Australia although it occurs there in the late Pleistocene.

Phascolarctidae

Koalas are diverse in Miocene deposits of interior Australia, but the earliest representative of the genus *Phascolarctos* occurs in the later Miocene Curramulka Local Fauna of coastal South Australia (Pledge 1992). A primitive early Pliocene species, *P. maris*, occurs in the shallow-water marine Loxton Sands in the Murray Basin (Sunlands Local Fauna, Pledge 1987). A species

of koala close to the living *Phascolarctos cinereus* is present in the late Pleistocene of southeastern Australia. The genus is not recorded in intervening deposits.

Ektopodontidae

Species of the genus **Darcus* are known only from Hamilton and another genus of this family survived into the early Pleistocene at Nelson Bay (M. Whitelaw, pers. comm. 1993) representing a relictual occurrence of an important Miocene group.

Phalangeridae

Members of this family occur in the early Pliocene: *Trichosurus* sp. at Boxlea, and *T. hamiltonensis* and *Strigoscus* **notalis* occur together at Hamilton. In the late Pliocene, *Phalanger* sp. is recorded at Dog Rocks.

Petauridae

Forms close to living small gliders are known from Hamilton largely because of the intensive screen-washing there. A *Petaurus* sp., close to *P. norfolcensis*, also occurs in the late Miocene Curramulka Local Fauna of South Australia (Pledge 1992). Pseudocheirines are somewhat larger forms and thus have a wider record before the late Pleistocene in southeastern Australia. The early Pliocene Hamilton Local Fauna contains two extinct *Pseudocheirus* species, one that appears to be related to the living *Petauroides* (*Pseudocheirus* **stirtoni*) and the other to members of the living subgenus *Pseudocheirus* (*P. *marshalli*). Two unidentified species of *Pseudocheirus* are present in the late Pliocene (Dog Rocks) and a species close to the living *P. peregrinus* is present in the early Pleistocene at Nelson Bay. The latter site also contains a new genus of giant pseudocheirine. Additional early Pliocene diversity in the ringtail group is also indicated by **Pseudokoala erlita*, known only from Hamilton.

Burramyidae

In the well-sampled Hamilton site a species of *Burramys* (*B. *triradiatus*) occurs in a rainforest setting near sea level. This genus is not further represented in southeastern Australia until the late Pleistocene when the living *B. parvus* appears in superficial deposits in caves in the Buchan district, Victoria, at about 600 m elevation. In the Holocene it retreated to above 1300 m to be associated with alpine environments.

Potoroidae

This family has a long Neogene record in central and northern Australia, the living genera appear in the Miocene in that region. The recently described Curramulka Local Fauna (Pledge 1992) of later Miocene age also contains an early record of *Potorous*. *Hypsiprymnodontines*, both *Hypsiprymnodon* sp. and the larger **Propleopus* sp., occur in the early Pliocene (Hamilton), and the latter also at Boxlea, perhaps the earliest record of the genus. **Milliyowi bunganditj*, a newly recognized potoroid of uncertain affinities, occurs only at Hamilton indicating some diversity within the group in the coastal early Pliocene. *Bettongia* sp. is known in the medial Pliocene in the Murray Basin (Fisherman's Cliff). By the close of the Pliocene *Potorous* sp. and a form near *Bettongia* are present in the Port Phillip Basin at Dog Rocks. These potoroid genera are common in the late Pleistocene of southeastern Australia.

Macropodidae

By Pliocene time most of the living genera of Macropodinae had appeared in the Australian record, as had most of those representing the diverse Sthenurinae. There are no living macropodine genera in Miocene sites. The record in southeastern Australia documents the loss of several early genera as well as early species of surviving genera during the later Pliocene. Genera whose living species have northern Australian and New Guinea distributions also fail to persist in the southeast beyond the medial Pliocene.

Sthenurine kangaroos such as **Troposodon* and **Simosthenurus* have later Miocene records at Curramulka in South Australia and early Pliocene records at Hamilton. **Troposodon* did not persist in southeastern Australia, but survived into the late Pleistocene in northern and eastern Australia. **Sthenurus* appears by the medial Pliocene (Fisherman's Cliff), and continues into the late Pliocene (Bone Gulch) and the late Pleistocene in the Murray Basin. Species of *Sthenurus* are present in the coastal regions in the late Pleistocene although they are not as diverse as in the inland. **Simosthenurus* species, such as **S. mccoysi*, that are close to later Pleistocene forms, are present in the medial Pleistocene of the Otway Basin. Species of this genus are most numerous in the coastal districts of southeastern Australia during the late Pleistocene.

Macropodines of the early Pliocene of southeastern Australia include extinct genera that did not persist into the later Pliocene; extinct genera whose early species did not persist into the

Pleistocene; living genera whose ranges contracted so that they were no longer present in the southeastern Australian Pleistocene, and living genera that continue to exist in southeastern Australia. Examples of the first are species of **Kurrabi* (**K. pelchenorum*) at Hamilton and **Kurrabi* sp. at Coimadai and Forsyth's Bank (Flannery *et al.* 1992). The second case is exemplified by early **Protemnodon* species such as the **P. chinchillaensis* that occurs in Kalimnan strata at Lake Tyers (originally identified as **P. otibandus*, Plane 1972, reidentified by Rich *et al.* 1991) and **P. cf. otibandus* at Hamilton. The last recorded occurrence in southeastern Australia of such early species of **Protemnodon*, is **P. devisi* from the Fisherman's Cliff Local Fauna of late Pliocene age in the Murray Basin.

Dorcopsis (*D. *wintercookorum*) and cf. *Dendrolagus* occur in the early Pliocene of the Otway Basin (Hamilton). *Dorcopsis* is also present in the western Murray Basin (Sunlands) in the early Pliocene. These living genera do not have later records in southeastern Australia. On the other hand species of *Thylogale* (*T. *ignis*), perhaps *Wallabia* and *Macropus* (*Notamacropus*) are recorded in the early Pliocene of the Otway Basin (Hamilton). In medial Pliocene time *Lagostrophus* sp. cf. *L. fasciatus*, *Petrogale* sp. and *Macropus* (*Osphranter*) sp. are present in the Murray Basin (Fisherman's Cliff).

Species of *Macropus* (*Macropus*) may be present in the early Pliocene (Coimadai), but a more secure record is present only late in the epoch at Dog Rocks in the Port Phillip Basin where species close to the living grey kangaroos (both *M. giganteus* and *M. fuliginosus*) occur. The occurrence of a skeleton of *Macropus giganteus* beneath basalt in the Great Buninyong Estate Mine, Victoria, implies significant antiquity for this taxon, perhaps predating 2.5 Ma, the age of basalt flows in the vicinity (Rich *et al.* 1991). The Dog Rocks site also produced the earliest record of *Wallabia bicolor* and a wallaby near *M. (Notamacropus) irma*, presently confined to Western Australia. A large **Protemnodon*, comparable to **P. anak*, succeeds earlier species in the late Pliocene (Dog Rocks).

By the beginning of the Pleistocene *Macropus* (*M.*) **titan* appears with **Protemnodon* sp. cf. *P. anak* at Duck Ponds, the earliest record of coexistence of two of the more common Pleistocene macropodid species. At Nelson's Bay the occurrence of **Baringa nelsonensis* indicates survival into the Pleistocene of a macropodine also known in the late Miocene Curramulka Local Fauna of South Australia.

The small samples available of medial Pleistocene faunas (Limeburner's Point and Hine's Quarry) indicate the continued occurrence of larger *M. (Macropus)* and **Protemnodon*, the presence of smaller *Macropus* species, *Wallabia* sp. cf. *W. bicolor* and *Macropus (Notamacropus)* sp. cf. *M. (N.) parryi* at Limeburner's Point and the possible survival of the northern Australian Pliocene **Prionotemnus* sp. at Hine's Quarry. Lack of Murray Basin sites of earlier Pleistocene age prevent establishment of the ranges of *Lagorchestes* and *Onychogalea*, genera that were common there in the late Pleistocene and Holocene.

Muridae

The array of small mammals obtained from the Hamilton site through intensive screen-washing lends credence to the absence of murid rodents there. Likewise the Miocene Curramulka Local Fauna lacks rodents although it has rodent-sized small marsupials. They have been reported from Parwan whose estimated age is 4.0 Ma., but supporting collections cannot be found in the Museum of Victoria. Thus the earliest verified occurrence in southeastern Australia is the material from the medial Pliocene Fisherman's Cliff Local Fauna in the Murray Basin. At that time the murids had achieved considerable diversity (Crabb 1976) and living genera such as *Pseudomys*, *Leggadina*, *Leporillus* and *Notomys* have been identified there. *Pseudomys* is also present in the late Pliocene (Dog Rocks) of the Port Phillip Basin.

IMPLICATIONS OF THE FAUNAL RECORD

Despite its obvious imperfections, the Pliocene-Pleistocene faunal sequence in the Murray and coastal basins of Victoria constitutes the most complete record of faunal change for that interval presently known on the continent. Central Australia (Lake Eyre Basin) and northeastern Australia (Charters Towers area) contain important dated early Pliocene assemblages, but large gaps separate these from younger Pleistocene faunas in the same districts. The record from the Murray Basin has a similar gap, but its medial Pliocene record nicely complements the coastal sequence. This is important as faunas on either side of this gap differ significantly through extinction, evolution and zoogeographic changes of their components. The evidence from the

Murray and coastal basins not only supports this conclusion, but allows us to chart the changes and provides a rough chronology for them.

Reassembling the faunal records temporally, three responses seem to be in play during a span of faunal change: 1) extinction of pre-existing taxa, 2) survival and, in some cases, evolution of pre-existing taxa, and 3) changes in geographic range of surviving taxa so that they become locally extinct. As the range chart (Fig. 3) indicates, important faunal turn-over occurred during the medial to late Pliocene. In the southeastern Australian early Pliocene a number of living and Pleistocene genera are already present, including *Antechinus*, *Sarcophilus*, *Strigocuscus*, *Vombatus*, **Diprotodon*, *Hypsiprymnodon*, **Propleopus*, *Dendrolagus*, *Dorcopsis*, **Protemnodon*, **Troposodon*, **Simosthenurus*, *Thylogale*, *Wallabia* and *Macropus (Notamacropus)*. **Euowenia*, **Darcus*, **Troposodon* and **Kurrabi* have records limited to the early Pliocene in southeastern Australia, while *Strigocuscus*, *Hypsiprymnodon*, *Dorcopsis* and *Dendrolagus* are not known in the region after the early Pliocene. However species of these living genera are restricted to northern Australia and New Guinea today, and **Troposodon* continued to be represented in eastern and northern Australian faunas into the late Pleistocene.

During the medial Pliocene in the Murray Basin additional living genera occur, some represented by species that appear limited to the Pliocene: *Sminthopsis*, *Dasyuroides* and *Dasyurus*, *Satanellus*, *Lasiorninus*, *Bettongia*, *Macropus (Osphranter)*, *Petrogale* and *Lagostrophus*. *Dasyuroides* and *Satanellus* are not known in younger faunas, but occur in northern Australia today. **Sthenurus* occurs first in the Murray Basin and becomes a member of the coastal assemblage by the late Pleistocene.

In the late Pliocene some living species, or forms close to them, appear in the Port Phillip Basin: *Vombatus ursinus*, *Wallabia* sp. cf. *W. bicolor*, *Macropus (Macropus)* sp. cf. *M. (M.) giganteus*, *M. (M.)* sp. cf. *M. (M.) fuliginosus* and *M. (Notamacropus)* sp. cf. *M. (N.) irma*. Some extinct genera must have undergone species level changes during this interval for by the beginning of the Pleistocene **Diprotodon optatum*, **Zygomaturus trilobus*, **Thylacoleo carnifex*, and **Protemnodon anak* appear in coastal Victoria. **Ramsayia magna* also appears in the late Pliocene of the Murray Basin. These taxa, along with *Macropus (Macropus) *titan*, are among the

most widespread components of the Pleistocene faunas of southeastern Australia.

In early to medial Pleistocene time some Tertiary relicts have their last appearances: *Ektopodontidae, **Baringa* and perhaps **Prionotemnus*. Further diversity is evident in living genera [e.g. *Macropus* (*Notamacropus*) sp. cf. *M. (N.) parryi*] and extinct forms such as "*Phascolomys*" cf. **medius* are present. Extinct genera such as **Simosthenurus* show initial phases of speciation (**S. mccoysi*) heralding their later Pleistocene radiation.

Palaeoecological interpretations from the mammalian fauna

Despite its inadequacies, the faunal evidence from southeastern Australia supports three general ecological conclusions. The first is that early Pliocene sites have genera whose living species are now members of the tropical rainforest assemblage, notably *Hypsiprymnodon*, *Dendrolagus*, *Dorcopsis* and *Strigocuscus* from Hamilton and *Dorcopsis* at Sunlands, suggesting similar environments prevailed in the Otway and western Murray basins at that time. Such taxa do not appear in younger Pliocene sediments of the coastal region, although there is a clear signature of relatively humid later Pliocene environments with *Vombatus*, *Potorous*, *Wallabia*, *Macropus* (*Notamacropus*), *Thylogale* and arboreal phalangerids and petaurids, all taxa that today inhabit wet sclerophyll forest.

Secondly there is an ecological contrast between the inland Murray Basin and coastal Victoria when comparable records are available in the medial to late Pliocene. Arboreal taxa are more commonly recorded on the coast, less frequently inland, judging from comparably collected sites (compare Fisherman's Cliff and Dog Rocks). Certain genera whose living species were widely distributed in the modern arid zone in immediately pre-European times (*Dasyuroides*, *Lasiiorhinus*, *Leggadina*, *Leporillus*), or are strongly represented in the arid-zone today (*Macropus* (*Osphranter*), *Petrogale*, *Notomys*, *Pseudomys*), are found in the Murray Basin in the medial to late Pliocene suggesting a climatic gradient similar in orientation to that of today.

A third conclusion is that the Pliocene assemblages of both the coastal and inland sites contain associations of living genera not known today. Flannery *et al.* (1992) point out the association of *Trichosurus* and *Strigocuscus* at

Hamilton as an example of taxa whose ranges do not overlap today, and the coexistence of *Hypsiprymnodon*, *Dorcopsis* and *Burramys* is another example from the same assemblage. Likewise, in the medial Pliocene of the Murray Basin (Fisherman's Cliff), *Lagostrophus*, *Dasyuroides*, and *Satanellus* are genera now widely separated zoogeographically. Such coexistence of taxa in communities that lack modern analogues (the "disharmonious associations" of Lundelius 1983) imply unusually patterned environments or subsequent adaptations of species of these genera to habitats occupied by their living representatives. The latter is clearly the case for the species of *Burramys*, as already mentioned.

Dated early Pliocene assemblages are known in central Australia (Tirari Formation local faunas, Lake Eyre Basin, Tedford and Wells 1992) and northeastern Australia (Bluff Downs Local Fauna, Queensland, Archer and Wade 1976). Both contain rodents and on this basis may slightly post-date the Hamilton Local Fauna. They are constrained by local geochronological indicators that suggest an age near 4 Ma for both areas. Except for the presence of a large *Dendrolagus* and the phascolarctid **Koobor* these northern faunas are dominated by terrestrial forms. The Pliocene genera **Euowenia* and **Kurrabi* are shared with southeast Australia and **Diprotodon* also occurs in the Tirari faunas. There are early Pliocene occurrences of living genera such as *Lagorchestes*, *Macropus* (*Osphranter*) and *Macropus* (*Macropus*), and extinct genera **Thylacoleo*, **Phascolonus*, and **Sthenurus* in the northern assemblages, the latter predates its record in southeastern Australia. The association of *Dendrolagus* with *Macropus* species and *Lagorchestes* has no modern equivalent but could indicate a vegetational mosaic, possibly riparian gallery forest and more open associations on river valley interfluvies, with the remains of taxa from parts of the mosaic being brought together by fluvial agencies. The comparison between southeastern and northern Australian Pliocene faunas suggests different zoogeographic patterning, broader mesic environments and less climatic diversity than present today.

Palaeoecological interpretations from geological history and the palaeobotanical record

Comparison of the faunal succession and its palaeoecological interpretation with physical and

other biological events in southeastern Australia indicates sufficient congruence in the timing and nature of change to suggest global controls of the events. Brown and Stephenson's (1991) masterful synthesis of the history of the Murray Basin is heavily drawn upon in the following account.

A hiatus of about 4 M.y. accompanies the late Neogene regression in the Murray and coastal basins during which these basins were emergent for much of the late Miocene. The sea withdrew beyond the present coastline, possibly to the continental edge, and the Murray Basin environment in particular became continental. Martin's (1987) study of the vegetational changes in the Lachlan Valley in the eastern Murray Basin shows that this period of emergence is accompanied by the first appearance of wet sclerophyll forest following a long Palaeogene and early Neogene occurrence of rainforest formations in the basin. The Curramulka Local Fauna of Yorke Peninsula, South Australia belongs to this regression. The cave system from which the fauna was recovered was open to the surface and collecting terrestrial debris during a period of lower water table. Lack of rainforest taxa in the assemblage perhaps reflects the drier environment in the karstic uplands of the peninsula.

The subsequent Pliocene transgression in the Murray Basin was accompanied by deposition of the shallow-marine Bookpurnong Beds followed by the marine Loxton Sand. During this high stand of sea level, rainforest vegetation redeveloped in the eastern part of the Basin. Martin (1937) has shown that although this forest contains *Nothofagus* species, only the temperate species groups are represented and these may have been restricted to the uplands surrounding the basin and to the more protected river valleys. Judged by its mammalian inhabitants, early Pliocene lowland rainforest of southeastern Australia may have resembled present-day rainforest of northeastern Australia. The few terrestrial fossils obtained from the Loxton Sand in the western part of the basin (Sunlands Local Fauna, Pledge 1985, 1987) include a large koala (*Phascolarctos *maris*), *Dorcopsis* sp. and a *zygomaturine diprotodontid. This assemblage may be approximately correlative with the Hamilton and Forsyth's Bank local faunas in the Otway Basin and the Lake Tyers Local Fauna in the Gippsland Basin, all occur in the transgressive phase of sedimentation (the Kalimnan Stage) in their respective basins. These assemblages are the only Pliocene faunas containing rainforest taxa.

When the sea withdrew from the Murray Basin

in the early Pliocene, strandline dunes followed (Parilla Sand) and finally fluvial deposits (Moorna Sand) penetrated interdune regions as regional drainage was re-established. Increasingly continental conditions in the Murray Basin were accompanied by the final demise of the rainforest and myrtaceous sclerophyll vegetation reappeared in the basin (Martin 1987). The Fisherman's Cliff Local Fauna was contemporaneous with this phase of regression and reflects the change to drier environments. Judged by the development of silicified ferruginous soils on the stabilized regression surface (the Karoonda Surface of Firman 1966), the climate included higher, and perhaps less seasonal, rainfall and temperatures higher than present.

In the Otway Basin the regression was accentuated by tectonic and thermal uplift accompanying the onset of the volcanism that built the Newer Volcanic plateau of western Victoria. The Port Phillip Basin forms part of the hinge zone between the Otway and Gippsland Basins. Its geological history resembles the latter, but late Neogene sequences are thinner and Newer Volcanic flows punctuated the section during the Pliocene. In the Port Phillip Basin the early Pliocene regression was accompanied by dissection of the Kalimnan transgressive sands (Moorabool Viaduct Sand). Backfilling of the erosion surface by thin marine deposits containing faunas attributed to the Werrikooian Stage (Carter 1985) and terrestrial deposits with the Dog Rocks Local Fauna, represent a short-lived late Pliocene transgression. This has its equivalent in the Murray Basin in the Norwest Bend Formation that was limited to the westernmost part of the basin. This was the last marine incursion onto the southern part of the continent. Thereafter Quaternary eustatic transgressions were confined to more coastal districts.

In the Murray Basin late Pliocene uplift of the coastal Pinnaroo block provided a tectonic dam limiting the sea and blocking the fluvial drainage of the Basin. These movements impounded the lower drainage of the basin's trunk stream (the Murray) and lacustrine claystone (Blanchetown Clay) accumulated in this large lake during late Pliocene through the early Pleistocene time (essentially the duration of the Matuyama Chron, An *et al.* 1986). Wet sclerophyll vegetation again occupied the eastern Murray Basin, responding to the humid conditions engendered by the large lake, itself mimicking the climatic effects of a marine transgression. Fluvial sand bodies reached into the lacustrine deposits as the lake

level rose and fell in response to climatic perturbations. One of these fluvial units (collectively the Chowilla Sand) contains the Bone Gulch Local Fauna of late Pliocene age. By the early Pleistocene rainfall diminished, evaporation rates increased and dolomitic limestones (Bungunnia Limestone) were deposited in the western part of the lake basin before an outlet was finally formed and the lake drained at about 0.7 Ma. The resulting increase in gradient entrenched the Murray River in its present course. Falling groundwater levels provided large expanses of unvegetated terrain that were available to aeolian processes under the increasingly drier and more seasonal climates of the Quaternary. As forest cover dwindled in the Pleistocene, woodland and grassland/herb fields developed as precipitation fell to modern values and beyond (Martin 1987). A fossil vertebrate record of this span of environmental change has not yet been found in the Murray Basin, the record continues there in the late Pleistocene after a substantial hiatus.

In the coastal district of Victoria late Pliocene through medial Pleistocene mammal faunas are present, and although the evidence is still sparse, it gives insight into the faunal changes during a span of important environmental change beyond that recorded in the Murray Basin. The Limeburner's Point and Hine's Quarry local faunas show that taxa common to the Late Pleistocene faunas of southeastern Australia already formed communities in the medial Pleistocene and continued through the rest of the Pleistocene without major change. Only the sthenurines seem to show increasing diversity of form as though this 0.7 M.y. span was a period of intense speciation.

Comparative palaeoenvironmental evidence is also available from the circum-Antarctic ocean (Hodell and Venz 1992 and references therein) and the Antarctic continent itself (Ishman and Rieck 1992 and references therein) covering the Pliocene and early to medial Pleistocene. These data indicate that the early to medial Pliocene seas were relatively warm with high sea-levels drowning coastal valleys in Antarctica and corresponding to the transgressive phase of Pliocene history in southeastern Australia. At approximately 2.6–2.4 Ma, at the beginning of the late Pliocene, a significant shift in $\delta^{18}\text{O}$ of both planktic and benthonic foraminifers toward positive values heralds the beginning of a major cooling in Antarctica, an event coincident with the initiation of the first major build-up of ice at high latitudes in the northern hemisphere. The resulting sealevel

drop is recorded as the post-Kalimnan regression in southeastern Australia. Cooler climates marked the demise of significant tropical rainforest in southeastern Australia and the return to temperate sclerophyll vegetation on the coast and more open formations inland. This early glacial-interglacial cycling was of irregular frequency allowing minor transgression (Werrikooian) in southeastern Australia, but by 1.4 Ma, in the early Pleistocene, a strong 0.041 M.y. cycle becomes evident in the $\delta^{18}\text{O}$ signal and this feature, associated with variation in the earth's obliquity cycle, persists throughout the Pleistocene. Thus early in the epoch Australia's biota was subjected to the climatic oscillations that were to typify the Pleistocene. Direct evidence of these cycles from the continent is woefully incomplete, but significant mountain glaciation in Tasmania reaches into the Matuyama Chron (Colhoun and Fitzsimons 1990) in agreement with the limits of such effects as determined from Antarctica.

CONCLUSIONS

Improved chronological resolution of the Pliocene and Pleistocene mammal-bearing deposits of southeastern Australia permits determination of the temporal succession of taxa and assessment of the zoogeographic and ecological significance of their occurrence. More comprehensive palaeomagnetic data, calibrated mostly by reference to radioisotopically dated flows of the Newer Volcanic field in Victoria, and more limited data from the Murray Basin, provide a chronology for the faunal succession from early Pliocene into medial Pleistocene time. Nowhere else in Australia is such a detailed representation of this interval to be found. Despite the preservational, taphonomic and palaeoecological biases of the record, it provides the best documented model of mammal faunal change at the end of the Australian Cainozoic.

Early Pliocene faunas in both the Murray and Otway Basins have greater affinity with Pleistocene and Holocene faunas than they do with known Miocene assemblages. Younger strata within the Pliocene transgression show many genera that represent the earliest members of lineages that persist through the Pleistocene and into the Holocene. In that sense the 'modern' fauna appears in the fossil record at the beginning of the Pliocene, but for some genera, their evolutionary appearance may considerably predate this first local appearance as suggested by the

Curramulka Local Fauna (Pledge 1992) of nearby South Australia. The late Miocene hiatus in the southeastern Australian basins limits opportunities to discover the actual historical record there.

Early Pliocene faunas of southeastern Australia contain several genera that appear not to be members of younger assemblages including the diprotodontid **Euowenia*, the potoroid **Milliyowi*, the macropodine **Kurrabi* and perhaps the ektopodontid **Darcus*. During the span of the early Pliocene the genera **Zygomaturus*, **Diprotodon*, and **Propleopus*, appear in southeastern Australia along with species, some extinct, of the living *Antechinus*, *Sarcophilus*, *Vombatus*, *Trichosurus*, *Thylogale*, *Macropus* (*Notamacropus*), *Wallabia*, *Hypsiprymnodon*, *Dorcopsis*, *Dendrolagus*, and *Strigocuscus*. The latter four rainforest genera are unrecorded in later deposits in southeastern Australia, and the co-occurrence of species of some of these living genera represent associations unknown in living faunas. The early Pliocene marine transgression in the Murray Basin and coastal basins of Victoria brought humid conditions onto the continent and rainforest was present in southeastern Australia.

Medial Pliocene regression restored continental environments to the Murray Basin and species of the living *Dasyuroides*, *Satanellus*, *Lasiorninus*, *Bettongia*, *Macropus* (*Osphranter*), *Petrogale*, *Lagostrophus*, *Notomys*, *Leggadina* and *Leporillus* appear in response to drier environments. Establishment of a large lake system in the western and central part of the Murray Basin in the medial Pliocene allowed wet sclerophyll vegetation to invade the basin. These conditions persisted into the early Pleistocene before the lake system was drained and drier shrubland vegetation became more widespread.

The late Pliocene and early Pleistocene appears to have been a time when living species, or forms close to them, appear in the coastal regions. Species such as *Vombatus ursinus*, *Wallabia* sp. cf. *W. bicolor*, *Macropus* (*Macropus*) *giganteus*,

M. (M) *fuliginosus* and *M. (Notamacropus)* *irma*, or closely allied taxa, appear in the late Pliocene. By the beginning of the Pleistocene a number of extinct species appear in the coastal region, *Sarcophilus* **laniarius*, **Diprotodon optatum*, **Zygomaturus trilobus*, **Thylacoleo carnifex*, **Protemnodon anak* and *Macropus* **titan*, all of which persist through the Pleistocene as the characteristic large mammal suite in most Quaternary assemblages.

The 'modernization' of the mammal fauna during the late Pliocene to early Pleistocene interval corresponds with the increasing continentality of southeastern Australia and to the climatic changes toward modern environments that are observed world-wide as the rate of glacial-age climatic cycling begins to increase. The faunal turnover at the close of the Pliocene, roughly coincident with the initiation of bipolar glaciation, also introduced taxa into the region that had no close relatives there and that seem to be immigrants from drier environments already established elsewhere. Earlier Pliocene histories for some of these [e.g. *Lagorchestes*, *Macropus* (*Macropus*) and *Macropus* (*Osphranter*)] are present in inland Australia. Later in the Pliocene and Pleistocene environmental contrasts between coastal and interior southeastern Australia yield zoogeographic patterns similar to those of the present-day.

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STUDIES OF THE LATE CAINZOZOIC DIPROTODONTID MARSUPIALS OF AUSTRALIA. 4. THE BACCHUS MARSH DIPROTODONS – GEOLOGY, SEDIMENTOLOGY AND TAPHONOMY

JOHN LONG & BRIAN MACKNESS

Summary

The remains of at least twenty individuals of *Diprotodon* were excavated from the Hine's Quarry Fossil Site near Bacchus Marsh, Victoria over the 1973 and 1979 field seasons. Sediments entombing the fossils consist of closed framework sands and grits with interspersed clay lenses, which sit on top of the Tertiary Werribee Foundation. Sedimentary structures and comparison with recent sediments of the area indicate that the depositional environment was the proximal part of a low flow regime, ephemeral run-off system, containing an intercalated erosional scree suggestive of times of non-hydraulic influence. Bone orientations are related to channel morphology with minimal hydraulic action responsible for poor sorting into Voorhies groups. Bone surface textures and fracture patterns indicate possible carnivore gnawing and prolonged subaerial exposure in an arid climate. Articulated skeletons are common in the proximal area of the bone bed with reworked skeletal material distally. Regional lithologies were reviewed with respect to their contribution to the bonebed.

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LONG, J. & MACKNESS, B. 1994. Studies of the late Cainozoic diprotodontid marsupials of Australia. 4. The Bacchus Marsh Diprotodons – Geology, sedimentology and taphonomy. *Rec. S. Aust. Mus.* 27(2): 95–110.

The remains of at least twenty individuals of *Diprotodon* were excavated from the Hine's Quarry Fossil Site near Bacchus Marsh, Victoria over the 1973 and 1979 field seasons. Sediments entombing the fossils consist of closed framework sands and grits with interspersed clay lenses, which sit on top of the Tertiary Werribee Formation. Sedimentary structures and comparison with recent sediments of the area indicate that the depositional environment was the proximal part of a low flow regime, ephemeral run-off system, containing intercalated erosional screes suggestive of times of non-hydraulic influence. Bone orientations are related to channel morphology with minimal hydraulic action responsible for poor sorting into Voorhies groups. Bone surface textures and fracture patterns indicate possible carnivore gnawing and prolonged subaerial exposure in an arid climate. Articulated skeletons are common in the proximal area of the bone bed with reworked skeletal material distally. Regional lithologies were reviewed with respect to their contribution to the bonebed.

John Long, Western Australian Museum, Francis Street, Perth, Western Australia. Brian Mackness, School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, NSW 2033. Manuscript received 7 September 1993.

The remains of diprotodontid marsupials are commonly found in the Late Cainozoic deposits of Australia but normally comprise isolated elements such as jaws, limb bones or teeth. Whole skeletons including skull and mandibles are a much rarer occurrence but a number have been recovered including those of *Diprotodon* from Lake Callabonna (Tedford 1973; Pledge 1993; Tedford 1993); *Zygomaturus* from Mowbray Swamp (Scott 1915); *Euryzygoma* from the Bluff Downs Local Fauna (Mackness unpublished information) and *Neohelos* from Bullock Creek (Tom Rich pers. comm.).

A number of *Diprotodon* bones were first discovered at Hine's Quarry, 9 km south-west of Bacchus Marsh, central Victoria, in 1973 by Miss Kerry Hine. Subsequently the Museum of Victoria (then the National Museum of Victoria) began excavating a rich concentration of largely articulated *Diprotodon* skeletons, lead by Thomas Darragh and K. Simpson (Monash University). In 1979, further bones were uncovered by quarry work. Periodic field work was resumed under Dr. Tom Rich, Museum of Victoria up until December 1979 when the bone bed was completely dug out. During this time bone elevations and orientation relative to two fixed datum points were measured, and sediment samples were taken from the bone

bed and its surrounding outcrops, for detailed analysis.

Rich (1976) regarded the Hine's Quarry site as probably a channel deposit, and from comparison with the present level of the Parwan Valley suggested that the site could be relatively old. The only age control on the site is the Newer Basalt which is present within the fossil bearing sediments as cobblestones. The Newer Basalt lies above other lava flows in the region. The oldest of these flows has a maximum date of 4.03 million years (Rahman & McDougall 1972), thus giving a maximum age range for the deposit as somewhere from Pliocene to Recent.

This paper reports on the taphonomy of this fossil site, examining broadly the geological and biological factors which indicate the possible cause of mortality and subsequent prediagenetic events leading up to the death assemblage uncovered in the quarry. It is based largely on the work of Long (1979, Monash University 3rd Year field project). Future papers by Mackness will discuss the taxonomy and tooth variation of the Bacchus Marsh *Diprotodon* site as well as its associated microfauna. Few taphonomic or palaeoecological studies of Australian Pleistocene mammal sites have so far been carried out (Horton 1976; Horton & Samuel 1978; van Huet 1993).

METHODS

Bone orientations were measured by compass bearing to the long axis on each bone. Elevation was measured using a plastic tube filled with a dark liquid. The end of this tube was tied to the datum pipe, with the level marked and then a measuring pole placed on the bone. The free end of the tube was moved up or down until the marker level on the datum pipe was achieved, and then height of fluid level was measured above the bone and recorded.

Field mapping was carried out in the immediate vicinity of Hine's Quarry, and sediment samples were collected from nearby ephemeral streams and eroding gullies for comparison. Sedimentological studies were carried out by standard dry sieving procedures, thin sectioning, and differential thermal analysis (DTA), the latter carried out at the Mineral Physics Laboratories of the CSIRO, Port Melbourne. Bone surface textures were

studied with the aid of a scanning electron microscope, and analysis of the composition of fossil and fresh marsupial bone was determined by use of an electron microprobe. Sedimentological methods follow those of Folk (1961). The orientations of bones collected during the 1973 field season were determined from a series of detailed photographs taken by Ian Stewart. Abbreviations for specimen/sample numbers: P, Museum of Victoria; #, Field Number; MG, Monash University Department of Earth Sciences.

GEOLOGY

Hine's Quarry is situated in the south-eastern corner of the sunken Ballan Graben, which forms part of the uplifted block on the west of the Rowsley Fault, bounded to the south by the Brisbane Ranges, and to the north by the

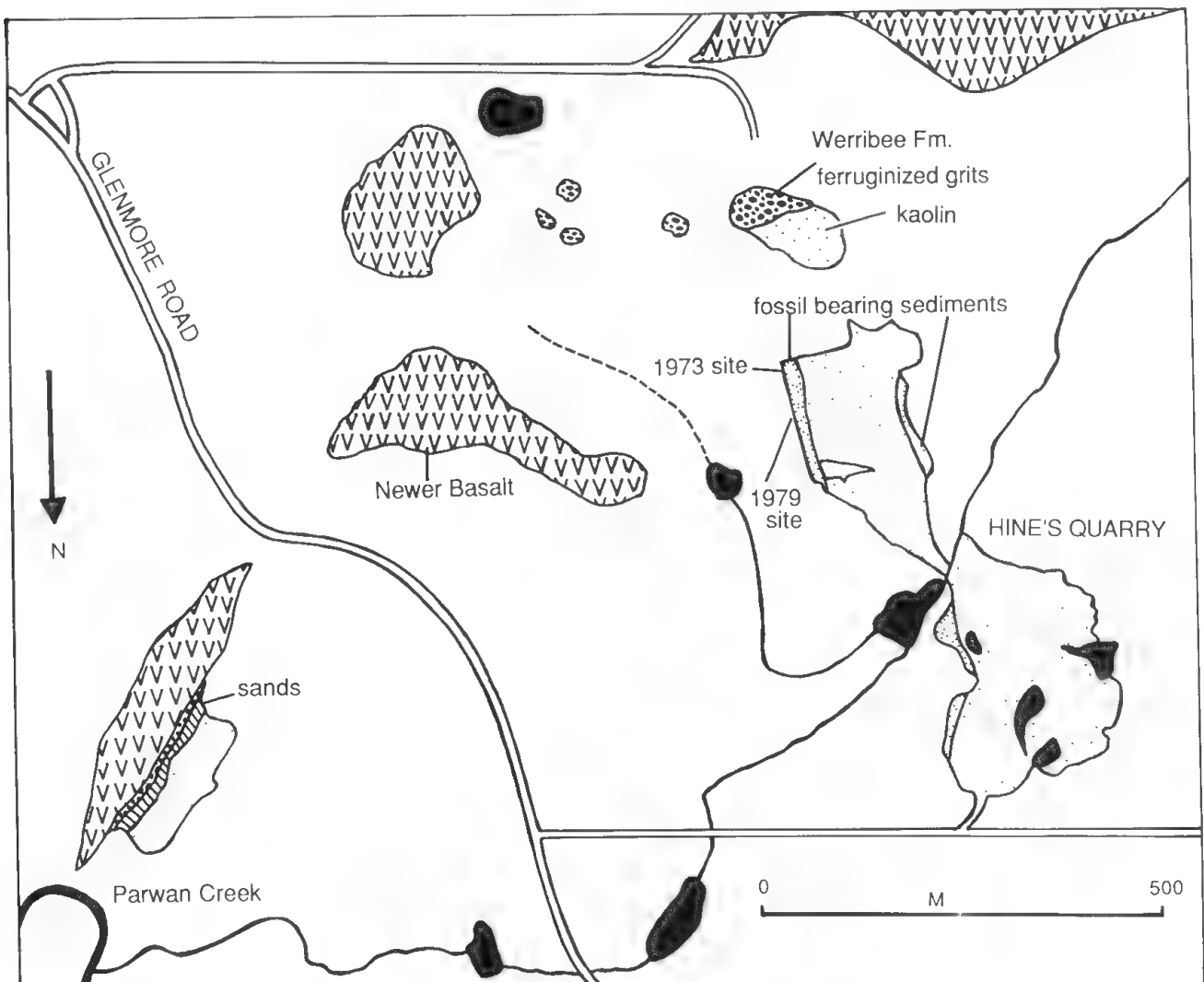


FIGURE 1. Local geology of the Hine's Quarry region, 9 km south-west of Bacchus Marsh, central Victoria, Australia.

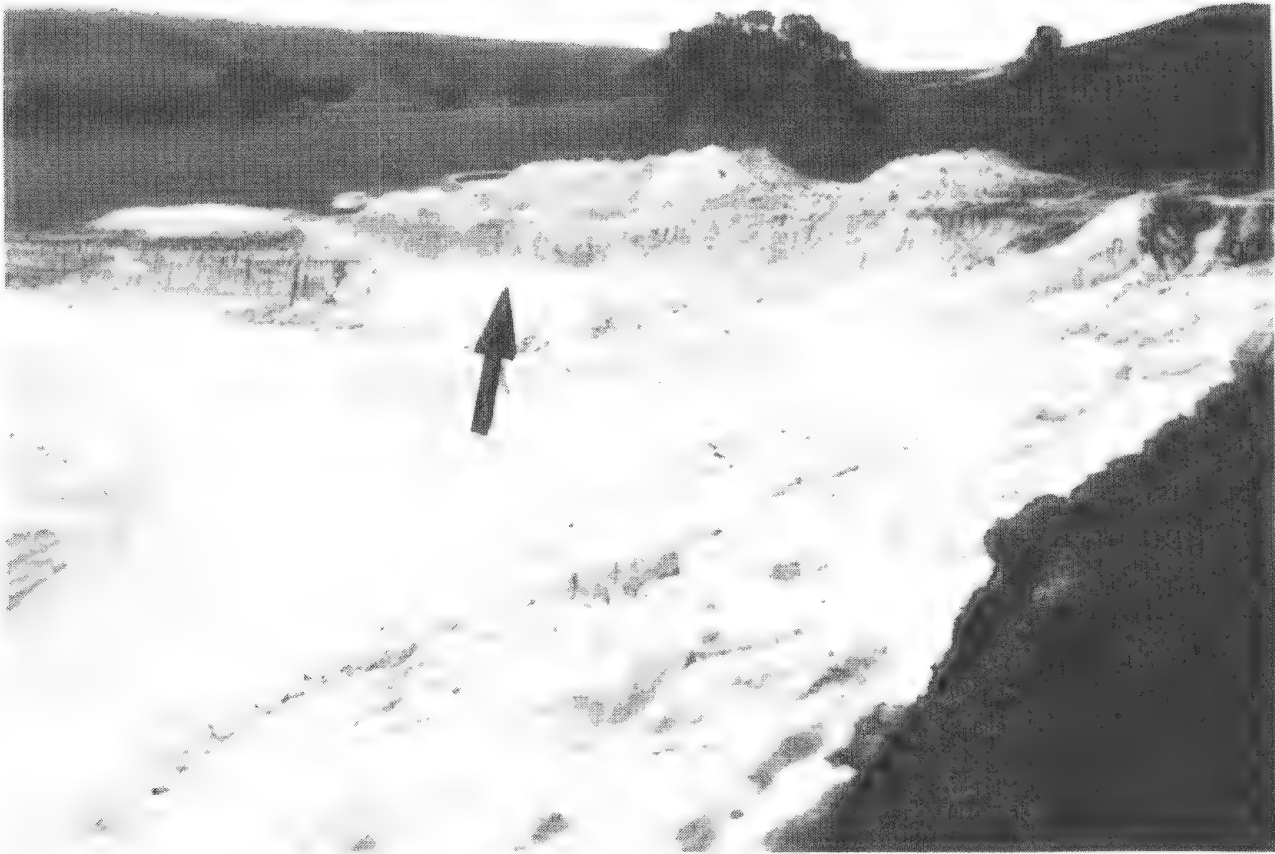


FIGURE 2. View of Hine's Quarry fossil excavation (arrow points to main bone horizon), looking east from the south-western corner of the quarry.

Lerderderg Ranges (Fenner 1918; Summers 1923). Parwan Creek and Werribee River cut into the soft clays and sandy clays of the Werribee Formation (Thomas & Baragwanath 1950; then called the Yaloak Formation), draining to the eastern lowland of the Werribee Plains. The fossil site (Fig. 1) is situated close to the Rowsley Fault which is post-Pliocene in age based on the evidence of faulted Newer Basalt dated at 4.03 million years (Rahman & McDougall 1972).

The fossils occur in the south-eastern corner of Hine's Quarry (Fig. 2) in a thin surficial layer of reworked sediments derived primarily from the underlying Werribee Formation. The Werribee Formation is made up of kaolin-rich sediments which (Fig. 3) are distinguished by their low quartz content, absence of basalt inclusions, and more compact texture. Inclusions within the Werribee Fm are infrequent, but quartz pebbles and gravel lenses are present, derived from nearby Permian glacials and uplifted Ordovician flyschoid sediments. Two important units of the Werribee Formation are exposed near the fossil site, both which have contributed to the composition of the

fossiliferous sediments. The age of the Werribee Formation is tentatively placed as being Paleocene to Mid Miocene based upon microflora from the Lal-Lal coal deposit (Cookson 1954, 1957), and relationships with the older basalts (Wellman 1974). Exposed portions of the Werribee Formation at Hine's Quarry are not fossiliferous.

Ferruginized grits are exposed to the south of Hine's Quarry, forming 'Hine's Hill'. These are closed framework quartzose, coarse sandstones and gravels, representative of fluvial channel sediments with interspersed minor conglomerates and cross-bedded sandstones. The unit exposed at Hine's Hill is approximately ten metres thick. The top of this unit is capped by recent, relatively unconsolidated fluvial conglomerates. The ferruginized grits sit conformably upon the fine kaolinites exposed in the quarry. No basalt caps Hine's Hill, it being of higher elevation than the surrounding basalt plain.

At Werner's Quarry, one kilometre east of Hine's Quarry, the ferruginized grits are seen above the kaolin and below the Newer Basalt flows, confirming that this unit is included within



FIGURE 3. Contact between reworked fossiliferous surface sediments and Tertiary Werribee Formation kaolin (arrow indicates unconformity). Note coarse basal gravels containing large basalt cobbles.

the Werribee Formation. There are palaeosols and laterite with accretionary structures, roughly spheroidal and inwardly zoned, between the grits and basalt. This resembles the Timboon terrain in the Parwan valley (Gill 1964).

Sedimentology

Although fossil bones were found at two sites within Hine's Quarry, the main concentration came from the south-eastern corner, the subject of this study. Another locality, 'Ian's Site', has produced a few bones from the top of the south-west face of the quarry. Both sites involve similar lithology and are probably contemporaneous.

The sediments entombing the main bone concentration comprise discontinuous layers of clay-rich closed framework sands, gravels and silts (Fig. 4). They represent a mixture of both depositional and diagenetic events. Large basalt cobbles occur randomly throughout the deposit, either as isolated stones without associated gravel, or within small conglomeratic lenses.

Below the bone-bearing sediments is the disconformable contact with the kaolinitic clays of the Werribee Formation, and above the unit are recent river terrace conglomerates, so close to the subsurface as to be incorporated as regolith. The fossiliferous unit is up to 3.3 metres thick at the distal end of the bone concentration. The concentration of *Diprotodon* remains form the only marker horizon within these sediments, although spasmodic isolated bones (generally macropodid remains) randomly occur at all stratigraphic levels.

Several profiles through the unit were measured and described. The discontinuity of sediment layers can be clearly seen from these sections (Fig. 4). Sedimentary structures were generally absent apart from horizontal discontinuous stratification, lensoidal and festoon cross-stratification. Rarer instances of small scale scour and fill channels, graded laminar bedding, and steep erosional surfaces were encountered. The high clay content of the coarser beds is due to secondary seepage of clay through the open pores of the sand. These sediments are strongly bimodal, and have been analysed with the diagenetically acquired fine fraction omitted.

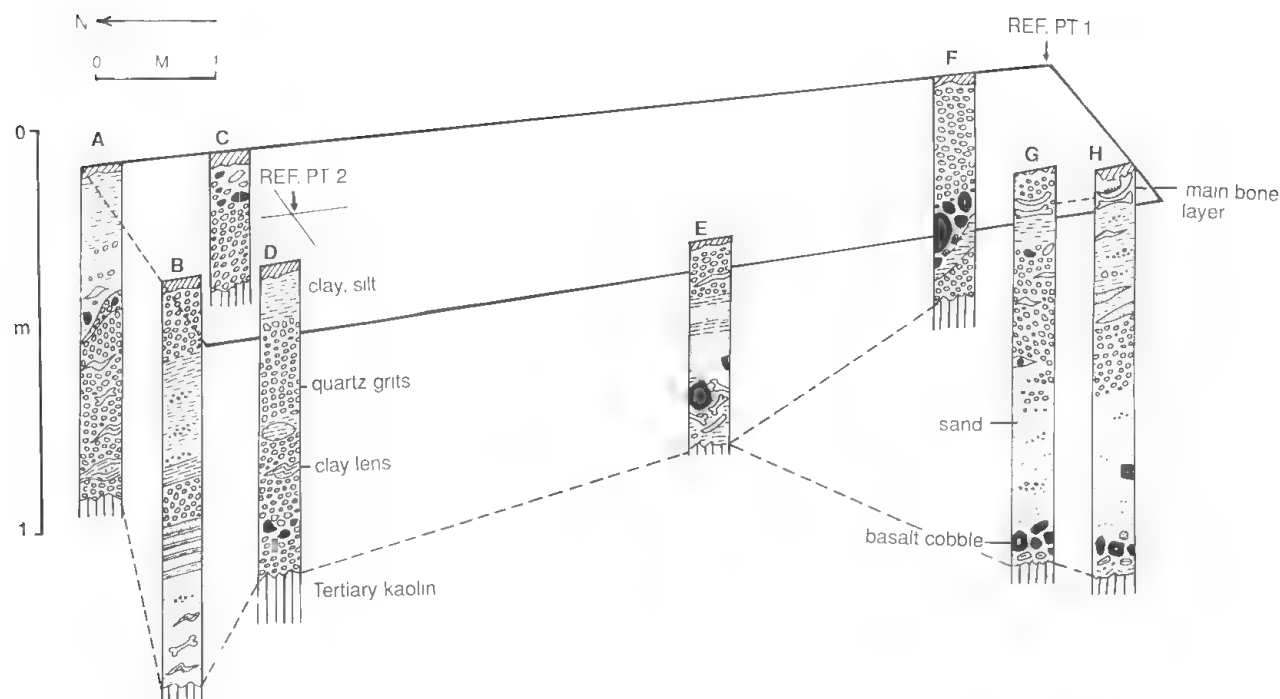


FIGURE 4. Profiles through the bone bed. Distance from Reference Point 1 to Reference Point 2, approximately 14 metres.

The dominant pattern is coarsening upwards, with coarse grits overlain by episodic fine silts and clays. Several depositional episodes are thus represented in the fossiliferous unit. The distribution of large basalt cobble is incongruous with the surrounding fine-grained sedimentary regimes. Apart from obvious association with sediments such as in basal erosional polymict conglomerate, the basalt cobbles elsewhere are randomly distributed. The composition of the basalt indicates it is from the nearby outcropping flows, and is also comparable in terms of deterioration. Smaller basaltic fragments in the fossiliferous unit (<2 mm) are severely altered by kaolinitization, recognisable only by the black specks of ilmenite and magnetite in a clay matrix. The weathered basalt clasts also showed vesicles.

The lowermost sediments of the fossil beds contain appreciable basalt, large pieces of ferruginized sandstone and intraclasts of dense, pure kaolinite. This clearly indicates erosion of exposed Werribee Formation (both kaolinitic clays and ferruginized sandstones) with input from the nearby eroding basalt plain.

Sediments of the bone bearing unit are mostly sand-sized once secondary clay content is extracted. The quartz content is of two types: orange quartz derived from the ferruginized grits, often cemented by iron oxides, and secondly, white quartz derived from the purer Werribee

Formation clays. The latter is hydrothermal quartz eroded from Ordovician sediments of the Brisbane and Lerderderg Ranges. Rare grains of plutonic quartz are also present. The quartz is mostly subangular. The only particles exceeding 20 cm diameter are basalt cobbles or *Diprotodon* bones. A typical section through the bone bed (Section E, Fig. 4) shows that the fossiliferous sediments are poorly sorted, platykurtic, near symmetrical medium to gravelly sands, with a 41–73% kaolin content.

Hypothetically the ferruginized grits capping Hine's Hill eroded back away from the quarry by gully, leaving steep, rilled, erosional faces. The base of this scarp has a build up of talus sediment. Sediments from the eroding gully talus and ephemeral valley stream near the quarry were analysed for grain size and composition (Figs. 5,6). The gully sediments are poorly sorted, mesokurtic, near symmetrical sandy gravels ($M_z = -0.98$) on top with poorly sorted leptokurtic coarsely skewed medium to fine sands below ($M_z = 1.32-1.92$). The ephemeral stream sediments are poorly sorted, near symmetrical, mesokurtic very coarse sands with appreciable (28%) gravel. A sample of surficial sediment from the quarry floor was also analysed, indicating a poorly sorted, near symmetrical platykurtic medium sand.

In all analyses the clay and silt fractions are very low. Sediments closest to the surface are

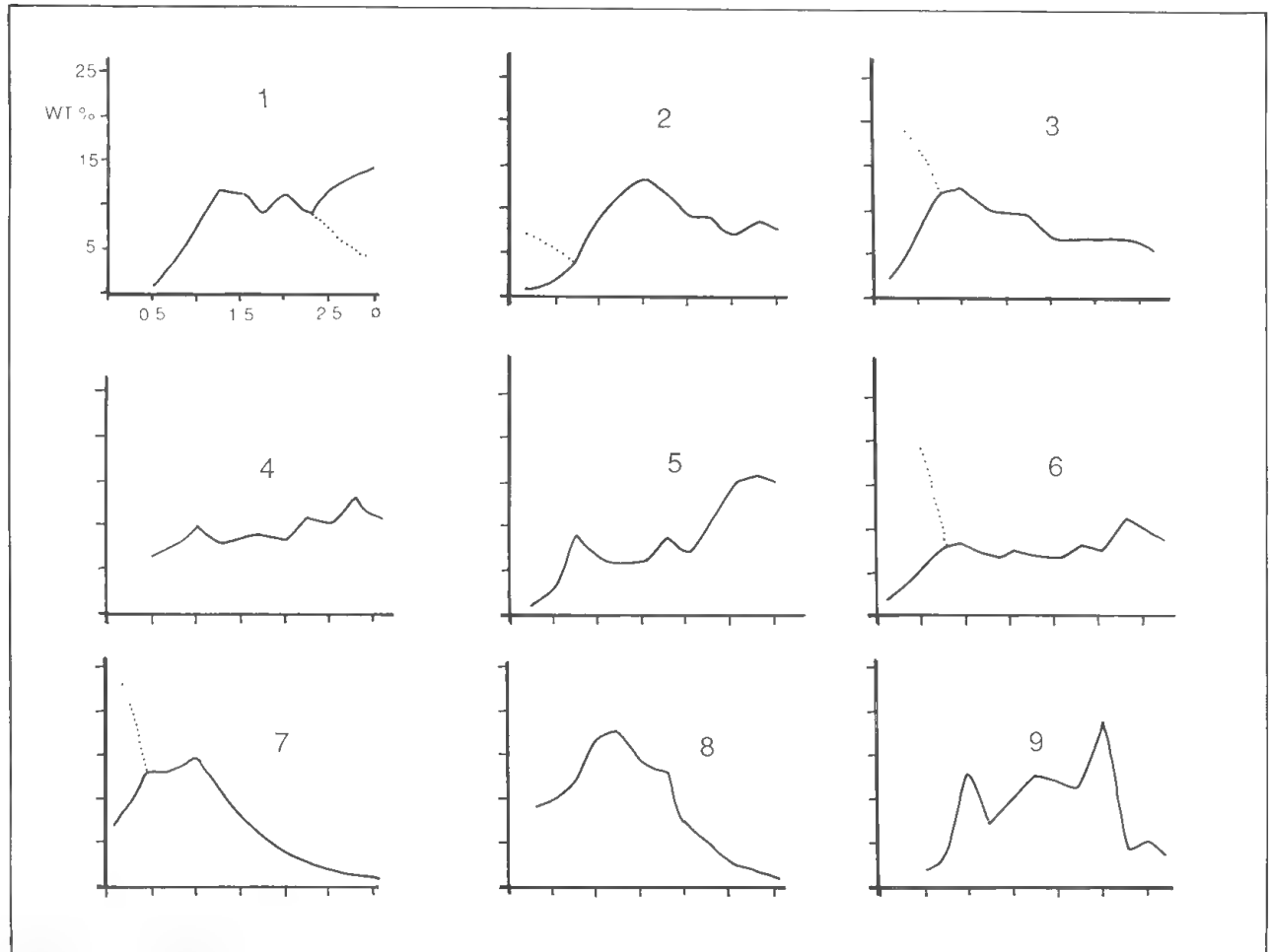


FIGURE 5. Sediment analyses from the bone bed (1–5), basement Tertiary Werribee Formation (6), and recent sediments near the fossil site (7–9). All to same scale, equal to axes of graph 1. Dotted lines indicate exclusion of secondary fine clays. All MG specimens: 1, –59442; 2, –59443; 3, –59444; 4, –59445; 5, –59441; 6, –59440; 7, –59438 (ephemeral tributary stream to the Parwan Creek); 8, –59434 (gully talus sediment); 9, –59439 (surface scree from quarry floor).

coarser and less sorted. Subsurface transportation of the kaolinitic fraction apparently occurs rapidly after erosion. The steep gradient of the bone bed, and the sedimentological analyses, indicate that the bones were deposited in an eroding gully and covered by surficial scree sediments and ephemeral run-off sediments, identical with those analysed from the vicinity of the quarry.

The shallow depth of the fossiliferous unit, together with its orientation parallel with the topographic surface, suggests it is a relatively recent accumulation, accruing over time by numerous episodic depositional events. Study of the bone surface textures (next section) supports the hypothesis that the surrounding sediment deposition was not a result of high energy, continual processes, but slowly accumulating processes. This would allow time for the bones to be subaerially exposed for a prolonged period of time and weather prior to burial.

TAPHONOMY

Bone orientation data and interpretation

Stereographic projections, equal area net, (Phillips 1971) of bone long axis (poles to bones) for the 1978–1979 excavations revealed no overall trends (Fig. 7). When proximal (upslope end), central and distal sections of the bone bed were examined separately a weakly defined trend was seen for the distal end of the main *Diprotodon* concentration as bimodally directional. This indicates that the highest degree of hydraulic sorting occurred at this end, that is the furthest downslope area from the proximal concentration of skeletons. The information is derived from small fragments of bones, mostly rib pieces of similar size and shape. This suggests that although a small degree of current sorting occurred here the orientation of bones forming the

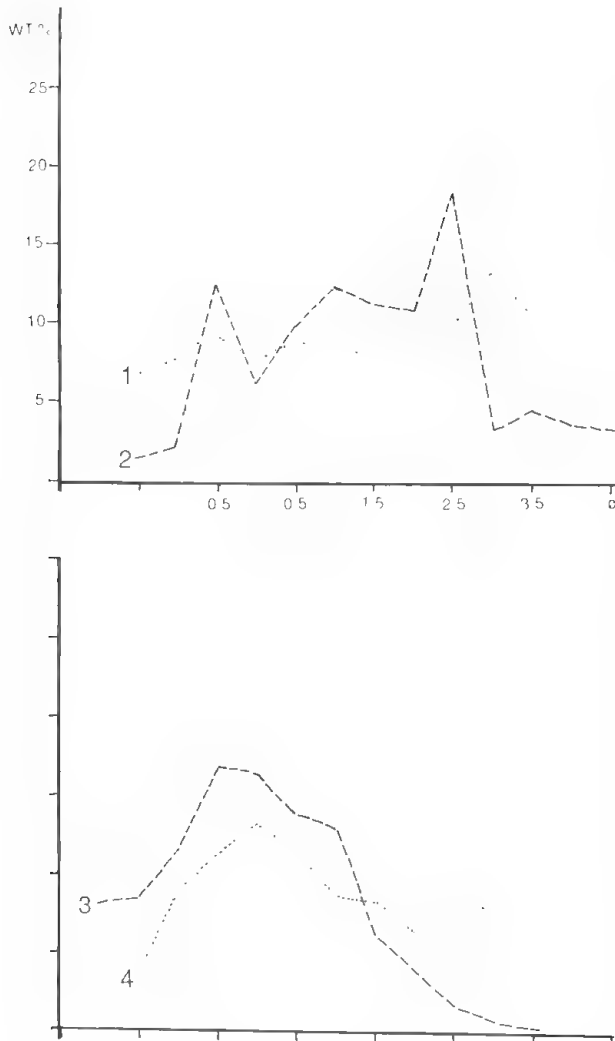


FIGURE 6. Comparison of recent sediments (2,3) with sediments of the fossil bed (1,4). All MG specimens: 1, -59445; 2, -59439 (surface scree, quarry floor); 3, -59443; 4, -59438 (ephemeral stream).

major portion of the bone bed was not influenced by hydraulic processes. Fig. 8 shows the overall plot of bone positions both horizontally and vertically in the bone bed, based on data from the 1979 dig.

Voorhies (1969) demonstrated that the bones from animals larger than sheep will act responsively to given hydraulic regimes, resulting in a sorting of bone groups from proximal to distal ends of stream flow. 'Voorhies groups' are associations of skeletal elements with similar hydrodynamic transportational properties. Group 1 contains vertebrae, ribs, sacra and sterna, and are considered the most easily transported, either by floating or saltation. Group 2 contains mostly limb elements, and group 3 contains the least mobile bones such as skulls and mandibles. Elements of group 2 move by traction whereas group 3 elements are chiefly lag components,

which remain closest to the site of death. Examinations of the distribution of Voorhies groups for the Hine's Quarry *Diprotodon* bed shows a concentration of 95% of group 3 bones at the proximal end of the bone bed. Most of the skull and jaw elements were closely associated. Fig. 9 shows a plan of bones from the central part of the bonebed reflecting the orientation of bones with respect to channel morphology. The individuals were very close to one another at the final place of deposition (Figs 10,11).

The roughly sequential array of Voorhies groups seen in the bone distribution map suggests only a minor degree of hydraulic transportation. The bone orientation data and sedimentological evidence indicates that ephemeral stream flows, of high energy but short duration, carried the partially articulated skeletons from the place of death to the main burial site. Subsequently erosional scree covered the exposed skeletons. The absence of large numbers of group one elements (for at least 22 individual *Diprotodon*) further supports the influence of rapid water flows for short durations, carrying most of these lighter bones away from the area which was excavated.

Bone orientations (Fig. 7) are generally horizontal to shallow plunging throughout the fossil bed, except for one localised concentration of steeply plunging associated macropodid bones in the north-eastern boundary of the bone bed. These bones rested in unstable positions with respect to gravity.

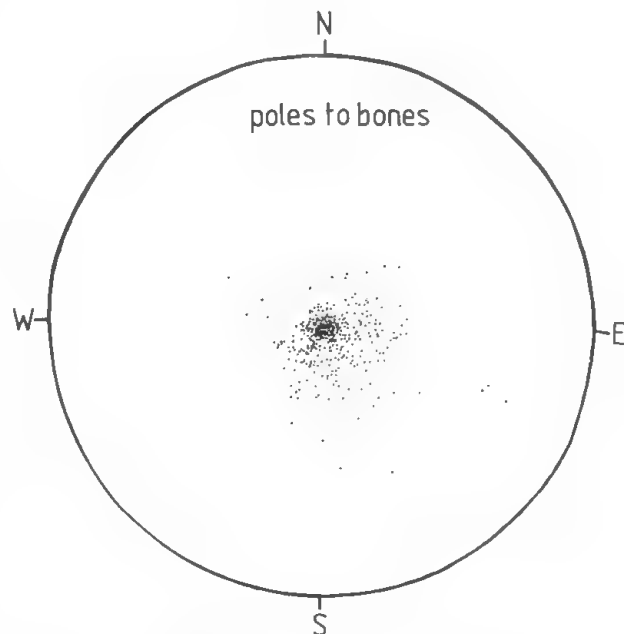


FIGURE 7. Stereoplot (equal area projection) of bone orientation from the 1978-1979 excavations. Note cluster of shallow dips and lack of bimodalism.

The high degree of bone articulation combined with their orientation suggests a separate episode from that of the original *Diprotodon* bone accumulation. Hypothetically a carcass dumped into an irregular erosional gully, somewhat like a pothole would produce a similar effect. Many of the isolated macropodid bones or partial skeletons occur at a different depth to the main *Diprotodon* bone horizon (Fig. 8) and are clearly separate burial events.

A contour map of the surface on which the bones were deposited was constructed (Fig. 9) from the elevations of the lowest bones in the main concentration of the bonebed. The channel (or channels) in which the bones were buried had an irregular morphology, often with V-shaped embayments upslope. The channel bottom was notched with local low and high spots. When bone orientations are studied in view of channel morphology it would seem that this factor had the strongest influence on the resting positions of bones. Bones caught in localised lows or runs have stronger preferred orientations according to the downstream flow of the channel than those dumped upon broad flat areas of the channel. High points are invariably devoid of bones.

Bone orientations are most easily explained in terms of channel morphometry, without indication of significant current sorting, save for the extreme

distal area of the bone bed. Sorting into Voorhies groups indicates spasmodic, short durations of concentrated high flow regimes, possibly flash floods washing carcasses down the gully channels. The main proximal concentration of articulated skeletons did not move far from the site of death, as indicated by their fine preservation and high degree of articulation.

The distal end of the bone bed terminates at the quarry scarp, and hence a large number of Voorhies group 1 elements are presumably missing from the excavated area having been washed away. The bone distribution map shows that there is a high density of bones proximal to the truncation of the bone bed, and it can be safely assumed that most of the fossil remains of Voorhies groups 2 and 3 were recovered by the excavations.

Bone preservation and articulation

Most of the bones have poor preservation, being soft and crumbly due to preburial weathering and diagenesis. Exposure of the bone before burial results in steady decomposition according to localised conditions (Behrensmeyer 1978; Behrensmeyer *et al.* 1979). The degree of bone surface decomposition ranges from Type 1 (Behrensmeyer 1978) (seen only in the proximal

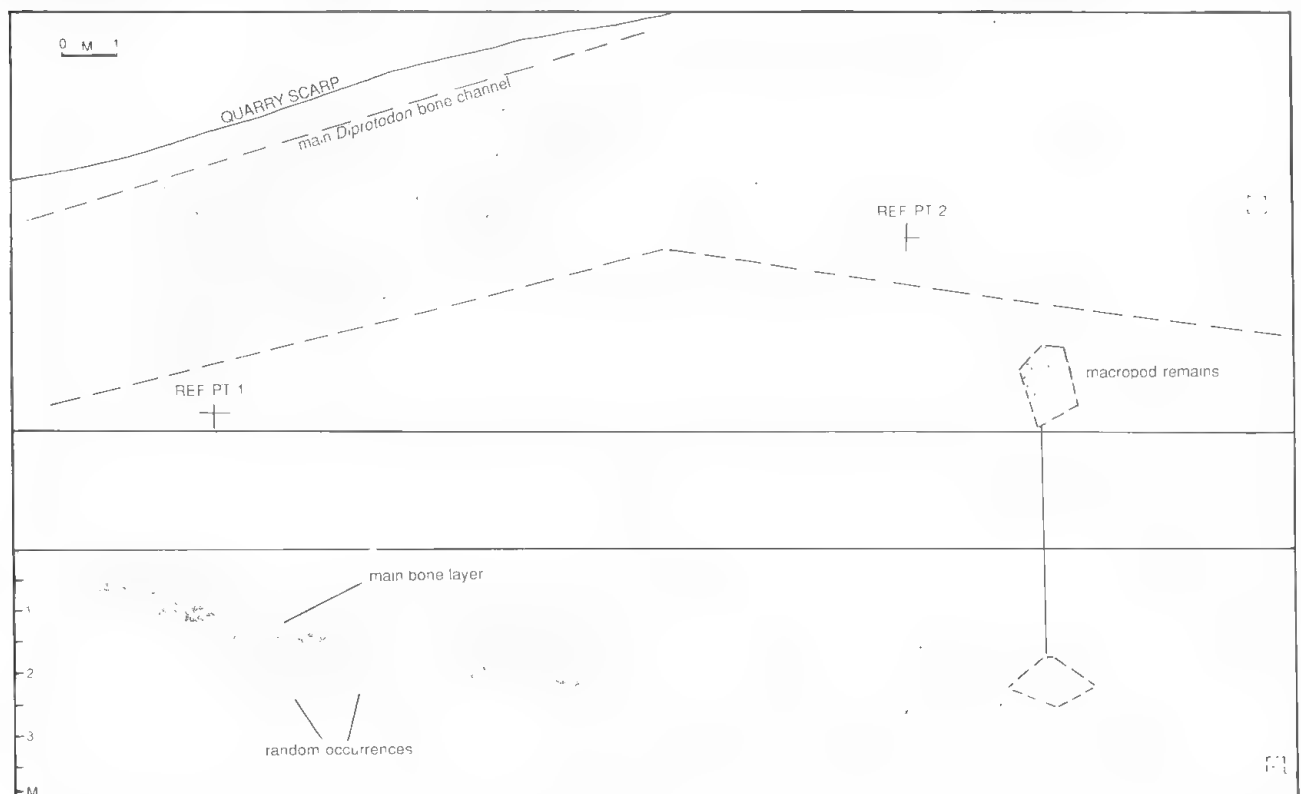


FIGURE 8. Distribution of bones from the 1978–1979 excavations. Top, plan view showing proximal channel outline. Bottom, depth of bone distribution.

region of the bone bed) to almost completely decayed pieces of bone, where the surface has been lost, showing only the spongy trabecular bone. Overall, most bones show surface flaking and cracking parallel to bone fibre, with a small degree of exfoliation of the outer surface,

corresponding to Types 2 to 3 of Behrensmeyer's scale (Fig. 13: 3,4). Comparison with the results from the Amboseli basin of Africa suggests that such bone has undergone prolonged exposure to arid climatic conditions.

Moisture accelerates bone decomposition, and

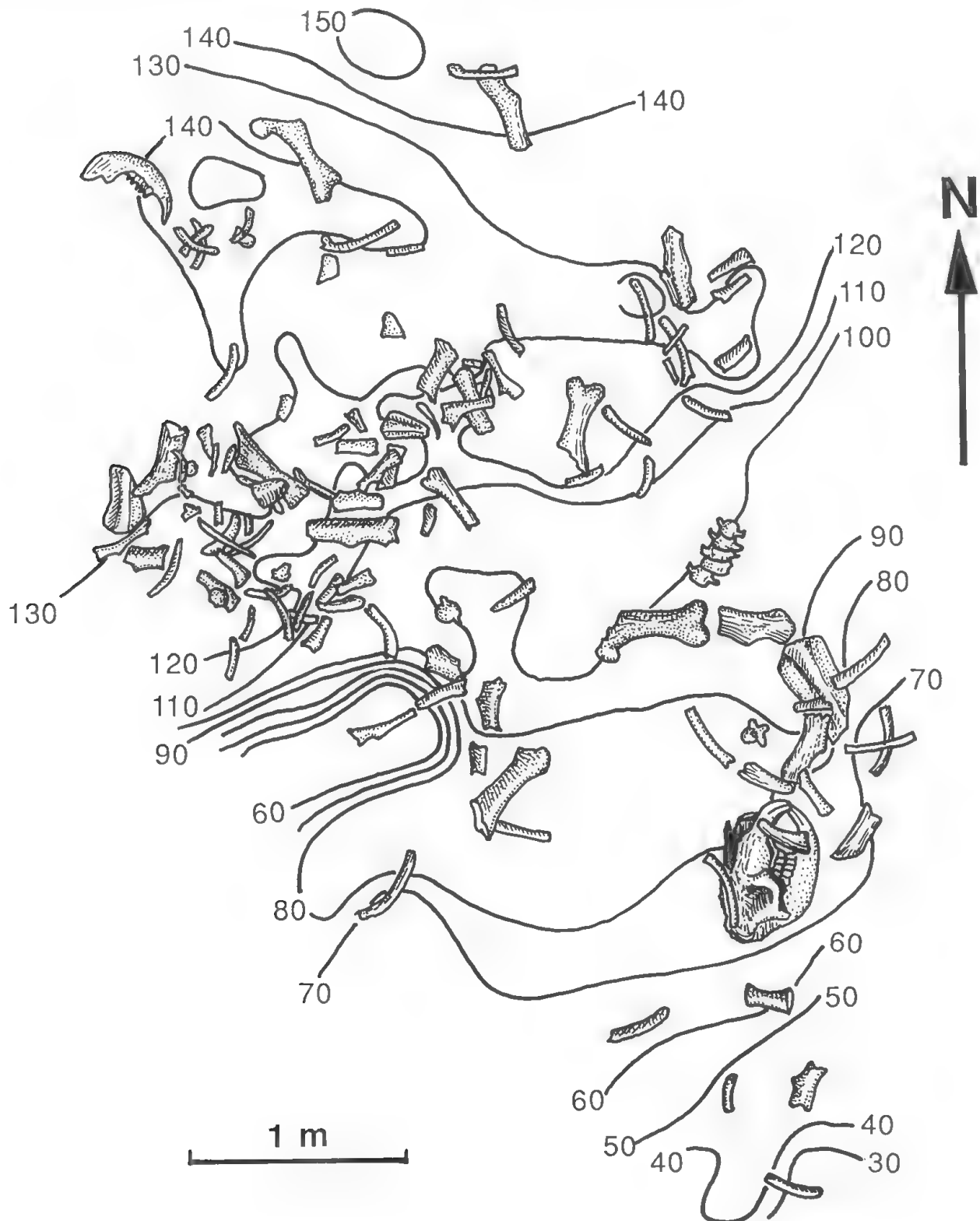


FIGURE 9. Channel morphometry shown in relation to bone orientation. Contours plotted by lowest bone depth from main concentration, bone orientations and preservation correctly shown.



FIGURE 10. Photograph from the 1973 excavation at the extreme proximal portion of main bone bed. Note excellent preservation, dense concentration and partial articulation of bones. Photo courtesy Ian Stewart.



FIGURE 11. Partially articulated skeleton in the proximal area of the bone bed, 1973 excavation. Photo courtesy Ian Stewart.

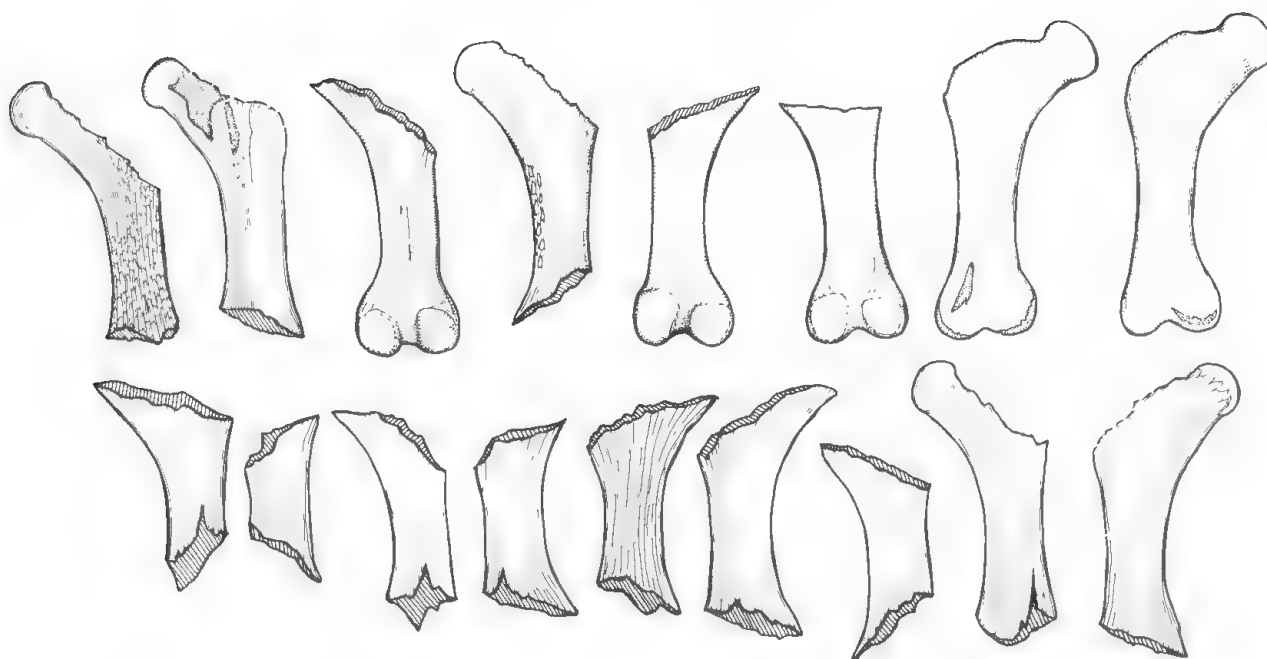


FIGURE 12. Bone preservation from the main bone bed. Seventeen *Diprotodon* femora showing degree of completeness and approximate state of surface condition.

decay of skeletons in temperate to tropical environments results in different styles of bone deterioration (Behrensmeyer 1975). Separate teeth of *Diprotodon* from the distal area of the bone bed show fractured roots and streaking of the enamel (Fig. 13: 1,2). Root fracturing is due to transportation, with significant preburial exposure causing enamel streaking and eventual splitting (Behrensmeyer 1978).

In general, the bones are recovered in variable states of preservation and degrees of articulation. The most proximal end of the bone concentration (1973 dig) shows a high degree of articulation, and relatively good preservation of bone surface (Figs 10,11). Articulation is not complete in any instance, the most complete skeletal remains comprise of skull, mandibles, vertebral column, parts of the limbs, shoulder girdle, pelvis and feet, not all articulated, but in close proximity. Skulls in the proximal area of the bone bed were often turned over, and one mandible was upside down resting in a steep position. Limb bones were always lying flat, as were scapulae and pelves. The strongly curved nature of the articulated vertebral column (Fig. 11) could indicate bending due to ligament contraction following drying of the carcass. The high number of skulls and mandibles recovered from this area, and the high degree of postcranial articulation, relative to that seen in the distal end of the bone bed suggests close proximity to the place of death.

The distal end of the bone bed is composed of

non-articulated limb and rib pieces, in variable state of preservation. Skulls and jaws were concentrated at the proximal end of the bone bed. One isolated skull was found very close to the distal end of the bone bed, and had presumably rolled down. Sections of articulated *Diprotodon* vertebral column were found only in the proximal half of the 1978–1979 excavation.

To conclude, the overall degree of articulation shown throughout the bone bed is not indicative of a natural trap or catastrophe in which animals are rapidly entombed whole (e.g. bogging, pitfall) but suggestive of mass mortality followed by exposure and some degree of transportation. At the proximal end of the bone bed some part of the skeletons were buried rapidly and show good surface preservation. The majority of the carcasses were disarticulated and moved slightly downslope.

Condition of the bones

Since the sediments of the bone bed were rich in kaolinitic clays, the diagenetic environment was basic (a solution of distilled H_2O with sediment MG 59443 was slightly basic, pH=7.5, although when made into a mud slurry with little water pH=9). High porosity of the grits in the bone bed enable concentrated basic condition for bone decomposition.

Microprobe analyses of fossil bone and tooth fragments from the bone bed show a slight increase in calcium oxide content, a decrease in

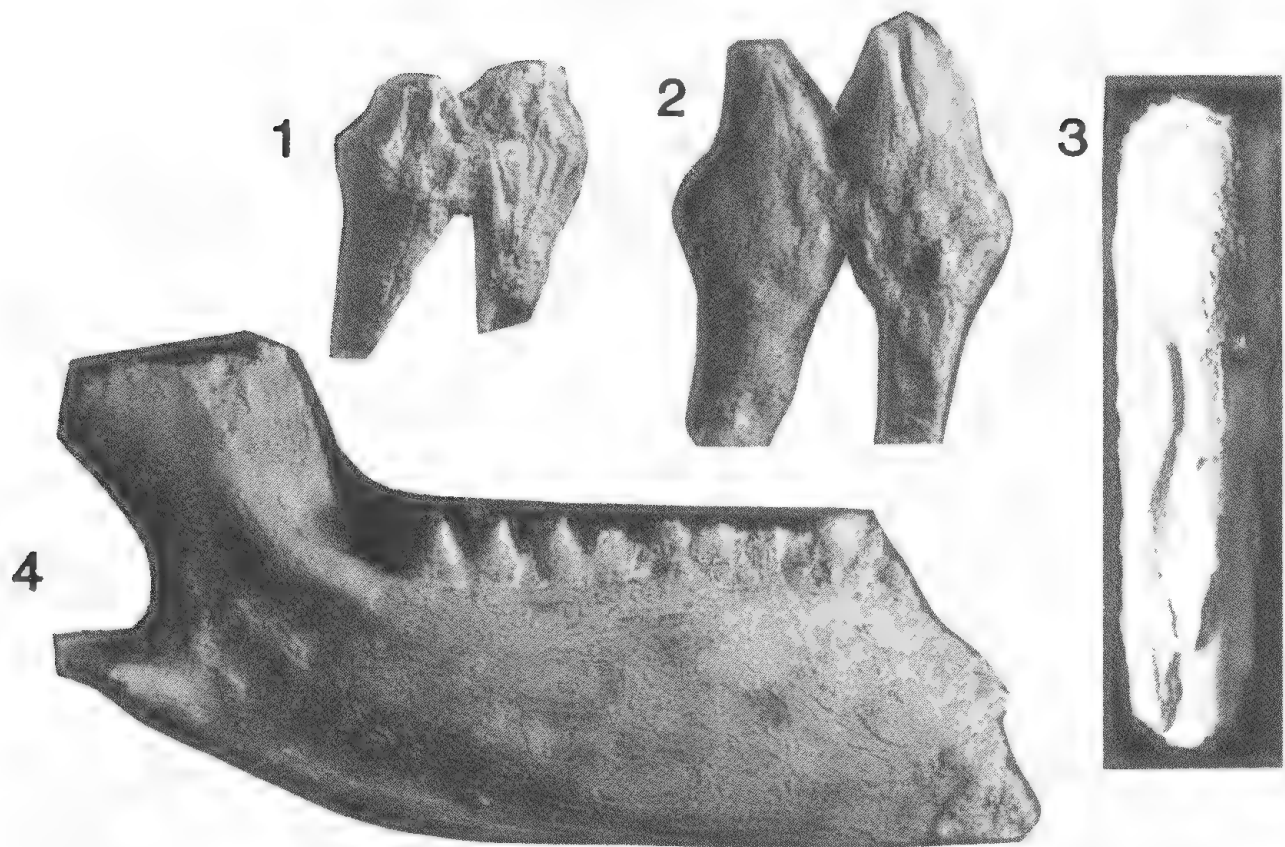


FIGURE 13. Bone preservation. 1–2, Isolated *Diprotodon* molars (no numbers) showing enamel streaking and splitting, with transportational abrasion to roots; 3, Highly weathered splinter of macropodid bone, showing parallel surface exfoliation, splitting and fracturing; 4, Macropodid jaw from the distal end of the main *Diprotodon* concentration. Note excellent preservation of posterior molars with splintering of premolar and anterior two molars. The ramus shows preburial exposure cracking and flaking, with transportational breakage to diastema and ascending ramus.

phosphoric oxide P_2O_5 with chloride salts added at 2–3% (relative to probed samples of modern *Macropus* bone and teeth). This indicates that the bones lacked mineralisation because of constant leaching or disappearance of available calcium oxide. Drying and wetting of the clays around the bones may have caused diagenetic fracture by swelling and compaction as host rock volume changes. Many bones had a coating of a black mineral presumably manganese salts.

Very few bones were preserved in their entirety, although those that were show only minor abrasive features such as rounding of edges. Vertebrae with entire neural arches typify this state, although they show gentle rounding of extremities. In a study of carnivore gnawing patterns on recent and Pleistocene mammals, Haynes (1980) documented the individual patterns of damage incurred upon each skeletal element when wolves utilised carcasses of medium to large-sized herbivores. Some of the Bacchus Marsh *Diprotodon* bones demonstrate similar damage patterns to those of bison scavenged upon by wolves.

Out of 28 femora examined only two were completely preserved without wear or breakage, apart from very slight abrasion of the greater trochanter (P 150114, and #94; Fig. 12). Three specimens showed good preservation of the trochlear area but had damaged greater trochanters or were lacking the femoral head. Light utilisation of bison femora by wolves results in damage to the greater trochanter only, followed by damage to the distal condyles and removal of the femoral head during heavy utilisation. The shaft may not be damaged as the end of the bone is softer, enabling easier access to marrow.

The majority of *Diprotodon* femora recovered from the site are missing both femoral head and trochlear region (Fig. 12). Fractures on the distal end of their shafts are screw type (Haynes 1980), suggesting transportation breakage. If gnawing had occurred prior to transportation then rounding of the edges, through abrasion, could have smoothed the jagged edges produced through carnivore action. Evidence of preburial scavenging is seen on some of the tibiae which hypothetically show gnawed off proximal heads (e.g. #67, #164,

#150, P150203).

Haynes (1980) shows articulated humeri with light carnivore gnawing, such as damage to the distal end, rather than the commonly gouged out and broken proximal epiphyses. The *Diprotodon* humeri showed much damage to the proximal epiphyses (#47, #157, #162, #257, #424, P151889, #218). Although no similar studies have been made on Australian carnivores, contemporaneous animals such as *Thylacoleo* were of suitable size and have left fossil evidence of predation on *Diprotodon* and other animals (Horton & Wright 1981; Runnegar 1983). Reptilian scavengers such as the giant varanid *Megalania* should also not be ruled out as contributing to post mortem bone damage.

The main bone concentration contains all the *Diprotodon* bones found, with only few additional macropodid bones, rodent remains and a lizard jaw. All other bones were found at various depths throughout the sediment, not confined to any single horizon or lithology (Fig. 8). A rodent maxilla was found in association with a partial macropodid skeleton in the distal part of the site.

In summary, both the state of bone preservation, bone fracture patterns and the distribution of taxa throughout the sediment suggest that some bones were transported and subaerially exposed longer than others. Different burial events are responsible for the main *Diprotodon* element concentration than for individual macropodid burials.

Bone settling velocities

Behrensmeyer (1975) formulated a method for calculating bone settling velocities in which bones were equilibrated to quartz pebbles sizes. For bones the size of *Diprotodon*, large quartz spheroids would be necessary. For example, a hippopotamus premolar has a quartz spheroid of 13.8 mm diameter as its hydraulic equivalent. Ribs of cows (*Diprotodon* size) require only 3.1 mm quartz equivalents. The flow of water moving the coarser quartz sands and grits of the bone bed may have just reached high enough energies to move ribs, but did not reach velocities capable of transporting larger skeletal elements by themselves. For vertebrae of about 29 cc volume (macropodid size) the hydraulic equivalent is a quartz spheroid of 4.4 mm diameter.

Most bones from the site have a much higher hydraulic stability than their entombing sediments, indicating close proximity and little transportation from the site of death. Movement to the distal area of the bone bed could have occurred either by

flotation of carcasses prior to decay, or have been assisted by the high slope gradient of the exposed channel, thus requiring lower flow regimes to achieve higher degrees of transportation.

Biological Data – population structure

At least 22 individual diprotodontids (based on numbers of right femora), all probably representing a single species of *Diprotodon*, were recovered from the site. A number of macropodids were also present as well as a variety of smaller mammalian taxa including rodents, dasyurids and peramelids. Fossils of reptiles have also been recovered.

It is clear from the tooth eruption and wear patterns of the Hine's Quarry *Diprotodon* that most were adults. Of the sixteen mandibles (Fig. 14) examined, most had all molars erupted and the majority of specimens lacked wear on both lochs of the fifth molar. Aged and juvenile individuals are absent.

The taphocoenosis (death assemblage) of the deposit is biased towards similarly aged individuals and excludes the very young and the very old. Such a selection could represent random sampling (normal rarity of juveniles or aged) or a biased selection of the strongest or most active animals. Similar age structure is described by Newsome (1965) in studying the reproduction of female red kangaroos in drought conditions. He noted that fecundity decreases during drought conditions and that adults in their prime constitute the dominant surviving group. The macropodid jaws from the deposit include at least two juveniles (e.g. MV-150120), although it must be pointed out that these apparently represent separate burial episodes from the main *Diprotodon* concentration.

DISCUSSION

Both the sediments of the bone bed and the distribution and orientation of the bones indicate that deposition occurred at the proximal end of an ephemeral stream system. The system envisaged would be at the foot of a series of gullied rilles running from the top of the hill (straighter at the proximal end) to the creek (increasing sinuosity distally). Evidence for this is seen by the discontinuous nature of bedding with lenticular and festoon cross-stratification. The latter indicates fluctuating sedimentary regimes and

moderate to lower flow regime (Dane-Picard & High 1973).

Thin wisps of almost pure clays and silts, occurring randomly throughout the bone bed are interpreted as depressions in the exposed surface where clays settled out of puddles following intense rains. This phenomenon was observed to occur in the quarry during fieldwork when 1–2 cm kaolinitic layers formed at the bottoms of puddles from overnight rain. It is because of the impermeable nature of the kaolinitic basement that the erosion of clays occurs. The presence of large basalt cobbles throughout the bone bed can be

explained by collapse and rolling of the nearby eroding basalt plain, hence the irregularity of the cobble size and distribution.

A close relationship is seen between sediments containing the bones and the modern sediments of the area. Mass percentage versus grain-size for some of these are identical. Sediment samples MG 59445 and MG 59439 (Fig. 5, graphs 4 and 9) are both polymodal with 4 peaks each, all corresponding to 1 phi size, most within 0.5 phi. Highest peaks are reached as 2.5 phi for 59439 and 3 phi for 59445. This demonstrates that the sediment containing the bones is little different



FIGURE 14. Sketches of tooth eruption patterns for sixteen individual *Diprotodon* mandibles. Where both sides were present the best preserved tooth is shown. 1, P151801; 2, P151802; 3, P150293; 4, P32223; 5, unnumbered; 6, P15106; 7–8, unnumbered; 9, P150017; 10, P151804; 11, #492; 12, P150062; 13, P150298; 14, P150299; 15, #25 (1973); 16, unnumbered.

from the surface wash scree on the quarry floor (MG 59439, Fig. 6, graph 2) which was derived from erosion of both ferruginized grits and purer sandy clays of the Werribee Formation. Comparison with ephemeral stream sediments near the quarry (MG 59438, Fig. 6, graph 4) indicates episodes of higher flow regime. Both MG 59438 (modern ephemeral stream) and MG 59443 (bone bed; Fig. 6, graph 3) are unimodal with closely spaced highest peaks at -0.5ϕ (MG 59438) and 0ϕ (MG 59443). Maxima for these samples are 16.7% and 13.2% respectively. This suggests that the sediment of the bone bed may have had a slightly lower energy of deposition.

The sediments entombing the bones signify a stream or gully system of generally low flow regime and fluctuating deposition. Erosional screes are intercalated with spasmodic higher flow regime channel sediments. Irregular channel morphometry and random bone orientation further supported by the steep channel gradient suggest a juvenile hydraulic system buried the carcasses. In summary the evidence does not favour a regular fluvial channel environment as first suspected, but an ephemeral erosional system.

The sedimentological data favours an arid climate at the time of deposition. Minimal predator influence corroborates the idea that aridity may have caused the death of a *Diprotodon* herd. Considering that the fossil-bearing sediments are close to the modern ground surface, the topography at the time of the event was probably not unlike the present condition. The eroded scarp of the ferruginized grits on top of Hine's Hill and the basalt would have been closer to the fossil site. The bone bed morphology is comparable to an eroding gully rille presently exposed above the fossil site, and the fact that the bones are channelled along a similar direction to the existing hill topography supports the recency of the event.

Ephemeral hydraulic regimes also support the aridity hypothesis, which would suggest an age for the site at the most recent late Pleistocene glacials (Bowler 1982). The phylogeny of the Diprotodontidae suggested by Stirton *et al.* (1967) restricted the genus *Diprotodon* to the Pleistocene, although the genus is also known from the late Pliocene Kanunka Local fauna (Tedford, Williams & Wells, 1986).

The scenario suggested by the combined data is that the herd of young adult *Diprotodon* expired from a period of severe aridity and drought. The carcasses were subsequently moved downslope after scavenging and extensive subaerial decomposition. The highly basic nature of the entombing sediment pore fluids caused a rapid deterioration of the fossil bones. The evaporation of ground waters during intense aridity resulted in the secondary infilling of kaolinitic clays in the pore spaces of the bone bearing sediments. This infilling was assisted by erosion of clay rich sediments from the surface which seeped downwards between pore spaces in following seasons of rainfall.

ACKNOWLEDGMENTS

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A NEW FOSSIL WALLABY (MARSUPIALIA ; MACROPODIDAE) FROM THE SOUTH EAST OF SOUTH AUSTRALIA

J. A. McNAMARA

Summary

A new wallaby, *Congruus congruus* gen. et sp. nov., is described, from a cave fill presumed to be of late Pleistocene age. While agreeing in some characters with many other macropodine genera, it most resembles *Prionotemnus* and *Protemnodon*.

**A NEW FOSSIL WALLABY (MARSUPIALIA; MACROPODIDAE)
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McNAMARA, J. A. 1994. A new fossil wallaby (Marsupialia; Macropodidae) from the South East of South Australia. *Rec. S. Aust. Mus.*: 27(2) 111–115.

A new wallaby, *Congruus congruus* gen. et sp. nov., is described, from a cave fill presumed to be of late Pleistocene age. While agreeing in some characters with many other macropodine genera, it most resembles *Prionotemnus* and *Protemnodon*.

J. A. McNamara, South Australian Museum, North Terrace, Adelaide, South Australia 5000.
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Mammal faunas from the cave fills of the Naracoorte area have been reported by Williams (1980), Wells *et al.* (1984) and Pledge (1990). These caves have yielded big samples of medium to large macropods, but, so far, few new forms have been reported, notably *Sthenurus maddocki* (Wells and Murray 1979) and *Sthenurus* 'P17250' (Prideaux *et al.*, in press). Just as the highly distinctive but apparently rare vombatid *Warendja* is known from four specimens from only two localities, so it might be expected that, as collections grow and are examined critically, specimens of rarer forms will be discovered.

The unique type specimen was compared directly with all specimens available in the fossil and modern mammal collections of the South Australian Museum. It was prepared by hardening with dilute Bedacryl after it was decided that it was too delicate to be safely handled; nor could a patina of fine sand, cemented with lime, be removed without losing bone. The teeth of the left-hand side were hand cleaned.

Tooth numbers follow Archer (1978). The composition of the Macropodinae used is that of Flannery (1989) but without *Hadronomas* (Murray, 1991).

Fig.2 contains an orientation symbol consisting of an arrow pointing to the anterior and an upturned U representing the tongue or lingual side.

SYSTEMATICS

Family MACROPODIDAE Gray 1821
subfamily MACROPODINAE Thomas, 1888

Congruus congruus gen. et sp. nov.

Holotype

P33475 (registered in the palaeontological collection of the South Australian Museum), a nearly complete adult skull with P³, M², to M⁵ both I² and left I³, missing anterior part of left nasal, the right zygoma, part of right temporal and mastoid. The incisors show moderate wear. P³ is unworn. The molars grade from the moderately worn M² to the unerupted M⁵.

Locality

S.O.S. cave (5U132) just south of Naracoorte in the South East of South Australia.

Age

Late Pleistocene by faunal association.

Etymology

From the Latin for agreeable or harmonious. Gender masculine.

Diagnosis

Congruus agrees in many of its character states with other members of the Macropodinae, but more closely resembles *Protemnodon*, *Prionotemnus*, *Kurrabi*, *Wallabia* and *Macropus*. It can be distinguished from the other macropodine genera by many characters, including lack of canine, long diastema, higher-crowned molars, entire palate and size.

Congruus is distinguished from *Protemnodon* by possessing a deflected rostrum; a P³ shorter than most molars (M³, M⁴, M⁵); a rather small masseteric process, not extending down to the line of the alveolar margin; and by lacking a large labial groove on I³.

It differs from *Prionotemnus* in possessing a more anterior placement of the infraorbital foramen; a less distinctly grooved P³, with a wider



FIGURE 1. *Congruus congruus* holotype skull P33475, x 0.75.

TABLE 1. Measurements (mm) of skull of *Congruus congruus* (P33475, holotype).

Description	mm
maximum length sans teeth	160.0
maximum height	59.4
maximum width of frontals	50.3
maximum width of nasals	36.7
length of diastema between alveoli	39.9
palate width at mid-diastema	20.8
rostrum width at mid-diastema	22.6
maximum width of occiput	21.8
width of postorbital constriction	31.2
height of premaxilla	30.7

longitudinal basin; a P³ shorter than M³; higher-crowned molars with longer, more procumbent anterior cingula; a forelink on M² and M³; and well-developed posthypocristae. It differs in lacking the deep groove well within the labial surface of I³.

From *Kurrabi* it may be distinguished by its relatively short P³; shorter, more anterior masseteric process; less elongate molars, having an oblique posthypocrista and lacking a distinct posterior fossette.

From *Wallabia*, *Congruus* is distinguished by its lacking a prominent labial groove on I³; well developed labial crests on all molars; and an anterior nasal spine. It is further distinguished by possessing procumbent incisors, an entire palate, a P³ shorter relative to the molars, with a smooth longitudinal basin; and by having the anterior portion of the brain case less constricted.

It differs from *Macropus* in lacking the distinct anterior (postorbital) constriction of the brain case; a groove on the labial surface of I³; a developed posterior fossette on the molars; and the inflation of the nasal part of the rostrum, relative to the anterior palate. *Congruus* is distinguished from *Macropus* by possession of more procumbent incisors; an entire palate; a well-developed ovale crest; oblique posthypocristae; and in having the loph-crests less bowed or preparacristae less developed.

Description

The skull, in general aspect, is lightly built, with a relatively large brain case, comparing in its gracility, with many living *Macropus* species.

From the side the skull presents a generally flat dorsal profile. The incisors and premaxillae are procumbent. No anterior nasal spine is present but in this position the premaxillae are smooth and depressed. The deep rostrum is arched dorsally and is near the plane of the flattened, somewhat

depressed frontal bones and the slightly raised frontoparietal region. The parietals decline towards a slight lambdoidal crest. A large diastema reveals a palate declining from a rather level cheek tooth row. The infraorbital foramen is above the anterior half of P³. The orbit appears relatively small and the zygomatic arch, light and shallow. The masseteric process is opposite the protoloph of M⁴, and small, not reaching the level of the alveolar margin.

From above, the rostrum tapers evenly forward from the lacrimals, and is flat sided without lateral inflation of the nasal part. The nasals have a broad, fairly straight contact with the frontals, on a line with the lacrimal foramina. The frontal bones are broad and flat, inflated laterally, above the orbit, and slightly depressed, centrally, on their common suture. The anterior part of the brain case is not greatly constricted postorbitally as it is in many macropodine genera. There is no sagittal crest and the temporal foramen is small.

From below, the incisive foramina are small. There are no canines. The palate, anterior to the cheek teeth, nearly equals the width of the rostrum above. The palate appears to have been entire. Pterygoid cavities, appearing small, have their lateral borders formed by prominent anterior-directed ovale crests. The alisphenoid bulla is slightly inflated and the auditory process is short.

Teeth.

I¹ is unknown but the alveolus is slightly larger than that of I², rounded, narrowed ventrally and not much compressed laterally.

I² shows no sign of an occlusal groove, perhaps, due to wear. The corresponding structure on I³ is attenuated and may indicate that the groove was much reduced or lacking on I². A broad shallow groove runs parallel and just anterior to the posterolabial edge, of I², which is raised and ridge-like.

I³ has a narrow and shallow occlusal groove

TABLE 2. Measurements (mm) of upper cheek teeth of *Congruus congruus* (P33475, holotype)

	Length	Anterior width	Posterior width
P ¹	9.8	4.6	5.0
M ²	8.6	6.9	7.1
M ³	10.6	8.1	7.8
M ⁴	11.5	8.6	8.2
M ⁴ (estimated)	10.4	8.9	8.0
P ³ - M ⁴	37.7	—	—
P ³ - M ⁵ (estimated)	48.1	—	—



FIGURE 2. *Congruus congruus* holotype P33475, stereopair of left cheek teeth, x 1.5.

which opens near the posterior edge of the labial surface so that the small lingual crest is barely visible and the groove so formed is barely visible on the labial surface. I have interpreted a pit, midway along the posterolabial edge of this tooth, as pathological but of localised effect and not associated with any general distortion of the crown – a view supported by the alveolus of the right I^3 which indicates a very similar tooth. It is probable that all the incisors were high crowned, and that, their relative sizes were $I^1 > I^2 > I^3$. Their combined outline in occlusal view was probably U-shaped.

P^3 is a little longer than M^3 . Its outline is not concave labially. There is a prominent labial crest with anterior and posterior cusps, with three indistinct cuspules and ridgelets between. There is a prominent posterolingual cusp, lower than the posterior cusp, and connected to it by a ridge, behind which is a small shallow posterior fossette. From the posterolingual cusp, a lingual cingulum runs forward, and is notched at one third of the tooth length, then is somewhat raised, before ending, almost opposite the anterior cusp. This cingulum, together with the main crest, forms a smooth longitudinal basin.

The upper molars are plain and quadrate, becoming more elongate and increasing in length from M^2 to M^4 and probably M^5 . The anterior cingulum is broad and shelflike with a shallow

basin between it and the protoloph to which it is connected by a preparacrista. A low forelink is present on M^2 and M^3 but not visible on M^4 or M^5 . The width and length of the anterior cingulum increases from M^2 to M^5 . The anterior width of M^2 is less than its posterior width but near equal in the other molars. The lophs have their apical width nearly equal to the basal width, not markedly narrower as in many *Macropus* and *Kurrabi*. A midlink is formed just lingual to the middle of the transverse valley by the postprotocrista, there is a small contribution from the metaloph. A shallow basin is formed in the transverse valley by an extension of the postparacrista on M^2 and M^3 , but not, M^4 and M^5 . The posterior face of the metaloph is rather plain and flattened, with a distinct posthypocrista rising obliquely to join the base of the metacone, where a small groove separates it from a much less distinct, near vertical, postmetacrista. Together they do not form a centrally placed fossette, seen in many forms, including *Macropus*, *Protemnodon*, *Thylogale*, *Wallabia* and *Onychogalea*. A much reduced postlink is discernible on M^4 .

DISCUSSION

The age of this material is inferred from its

association with *Thylacinus* and *Sthenurus* P17250 material with very similar preservation. This *Sthenurus* is known from the dated deposits of Victoria Cave (Wells *et al.* 1984) and the Henschke Fossil Cave (Pledge 1990), Naracoorte, and Green Waterhole (Newton 1988), Tantanoola.

Discovery of further specimens, particularly those with the lower dentition and deciduous cheek teeth, should add to the understanding of this form and, in particular, clarify its relationship to *Prionotemnus*.

One's attention is drawn to the prominent naso-frontal development of this species, which is presumably an autapomorphic character. Comparisons can be made with the similar structures found in *Onychogalea unguifera* and, if its function were known, it would allow conclusions about the functional adaptation of the fossil form.

In *Congruus* a combination of many primitive

macropodine features seem to be the foundation, overlain by apomorphy in the form of the whole skull giving it the general aspect of a modern-looking kangaroo. While this is adding to the increasingly large puzzle that is macropod phylogenetics, it is to be hoped that future study of this specimen will shed light on the major pathways followed by this family in its great evolutionary flowering through the latter half of the Neogene to the present.

ACKNOWLEDGMENTS

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CETACEAN FOSSILS FROM THE LOWER OLIGOCENE OF SOUTH AUSTRALIA

NEVILLE S. PLEDGE

Summary

A single, damaged cetacean tooth from the upper part of the Buccleuch Formation of the Murray Basin dates from the early Oligocene. It has been compared with Eocene archaeocetes and with late Oligocene cetaceans. Similarities are seen with *Mammalodon colliveri* and *Metasqualodon harwooddii*, but no definite assignment can be made.

CETACEAN FOSSILS FROM THE LOWER OLIGOCENE OF SOUTH AUSTRALIA

NEVILLE S. PLEDGE

PLEDGE, N. S. 1994. Cetacean fossils from the Lower Oligocene of South Australia. *Rec. S. Aust. Mus.* 27(2): 117–123.

A single, damaged cetacean tooth from the upper part of the Buccleuch Formation of the Murray Basin dates from the early Oligocene. It has been compared with Eocene archaeocetes and with late Oligocene cetaceans. Similarities are seen with *Mammalodon colliveri* and *Metasqualodon harwoodii*, but no definite assignment can be made.

A limb bone from rocks of similar age in the St Vincent Basin is described briefly, but cannot be ascribed definitely to any particular cetacean group.

Neville S. Pledge, South Australian Museum, Adelaide, South Australia 5000. Manuscript received January 1994.

Despite its vast areas and extensive sequence of Tertiary sediments (e.g. Ludbrook 1969), South Australia seems to be remarkably deficient in cetacean fossils. Most of these, usually just single or a few associated bones of cetaceans, have been found in lower Miocene sediments exposed in cliffs along the lower part of the River Murray. Discoveries are summarised in Glaessner (1955), Pledge and Rothausen (1977), Fordyce (1982, 1984) and Bearlin (1988).

One of these whales, *Metasqualodon harwoodii* (Sanger 1881), was found in the Wellington area of the River Murray, but its exact site, and consequently its precise stratigraphic horizon, was not recorded and has been the subject of some speculation (Pledge & Rothausen 1977). It was therefore with some excitement that the author received a primitive-looking cetacean tooth found by amateur palaeontologist and collector Mr D. J. Barrie in February 1989 at Fred's Landing, a few kilometres upstream from Wellington (Fig. 1). Closer examination, however, has shown the tooth not to be *Metasqualodon harwoodii*, but an older, possibly new taxon. Further excavation at the site failed to yield more cetacean specimens, but resulted in a rich, previously unknown, foraminiferal assemblage being recovered (Lablack, pers. comm. 19/2/91, 1991 unpublished report).

The specimens are registered with the South Australian Museum, Palaeontology Collections (SAM P). MUGD refers to specimens in the Geology Department of the University of Melbourne.

SYSTEMATICS

Class Mammalia

Order Cetacea Brisson 1762

Suborder *incertae sedis*

Genus and species indeterminate, A

Material:

The damaged crown of an anterior cheek tooth, SAM P34517.

Locality:

Fred's Landing, a boat launching area 3 km downstream from Tailem Bend, on the east bank of the River Murray. (Lat. 35°17'S, Long. 139°27'E).

Geology and Age:

The fossiliferous beds have a very restricted outcrop, but have since been recognised more widely in subsurface sections to the southeast.

The pale green, limonite-stained and slightly glauconitic, marly fine-grained limestone has a rich planktonic foraminiferal fauna, with key species *Guembelitria triseriata* and *Chiloguembelina cubensis* and associated species *Sherbonina atkinsoni*, *Gyroidinoides* sp. cf. *G. allani*, *Bolivinaopsis cubensis*, *Globigerina ciperoensis* and *Globigerina ouchitatensis* (Lablack 1991).

There is an invertebrate megafauna dominated

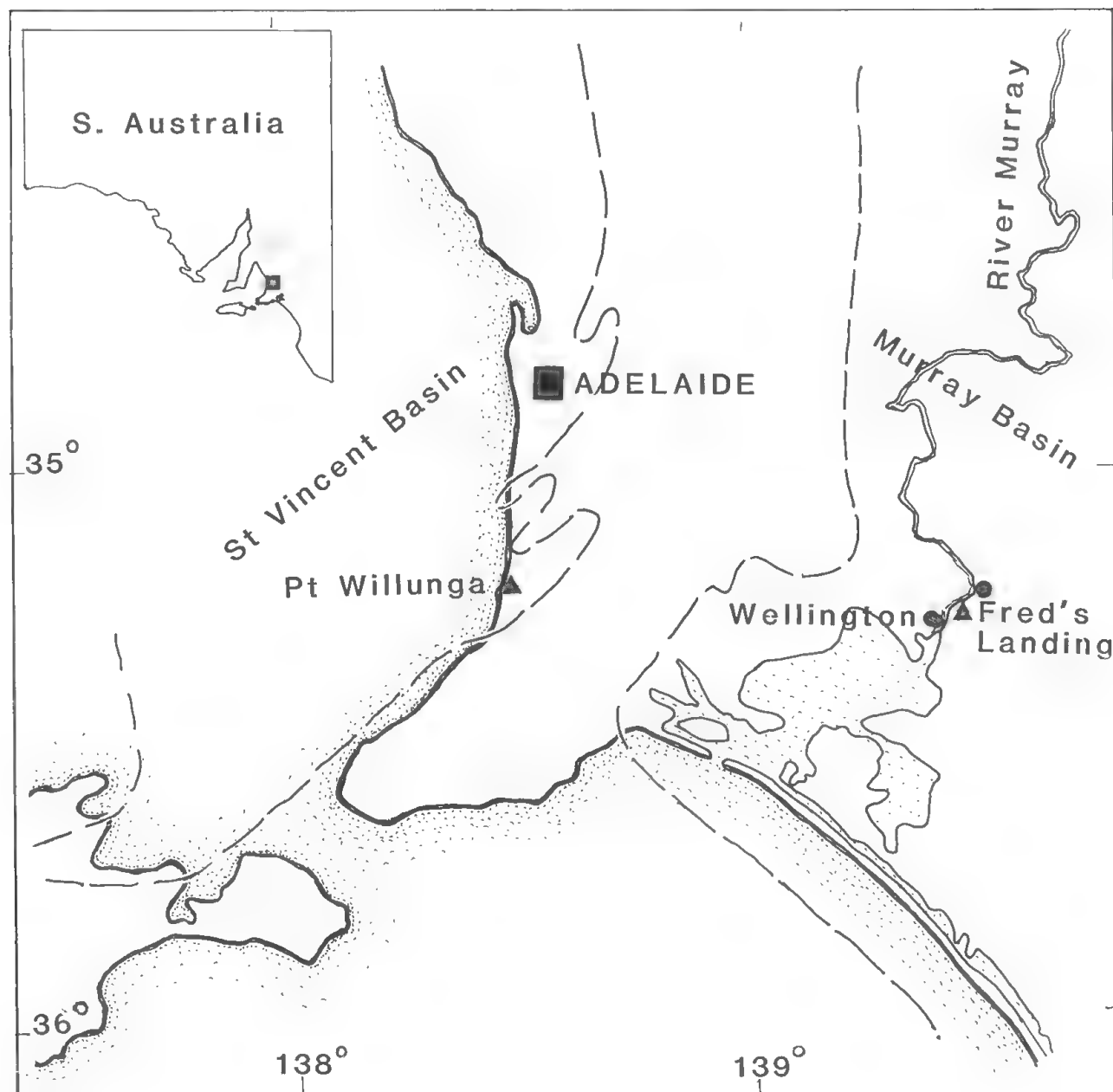


FIGURE 1. Locality map

by the small brachiopod *Murravia catenuliformis* and a small morph of the echinoid *Scutellinoides* sp. cf. *S. patella*, with occasional *Waldheimia* sp. cf. *W. insolita* and *Magasella woodsiana* (brachiopods) and *Corystus dysasteroides* (echinoid) fragments, *Graphularia* segments, small scallops (*Chlamys*), bryozoans and asteroid ossicles. There are also rare small shark teeth (*Lamna* sp. cf. *L. apiculata* and *Scapanorhynchus maslinensis*), and a broken teleost otolith. Unfortunately, none of these species is age specific, although *S. maslinensis* is found mostly in late Eocene formations (Pledge 1967).

Lithologically, the beds are similar to the Ettrick Formation (middle to upper Oligocene) which

occurs nearby. However, on the basis of the foraminiferal fauna, particularly *G. triseriata*, Lablack (1991 and pers. comm.) equated the unit in question with the lower part (Ruwarang to Aldinga members) of the Port Willunga Formation of the St Vincent Basin.

The planktonic foraminifera are more abundant in the Fred's Landing section than in the Port Willunga local type section for the South Australian lower Oligocene, where the sudden appearance of the key species *Guembelitria triseriata* (which has a restricted stratigraphic range in South Australia) marks the maximum flooding surface T4.4 of the major transgressive phase following the terminal Eocene regression

(McGowran *et al.* 1992). The presence of *G. triseriata* and *Chiloguembelina cubensis* together restricts the age to the early Oligocene (e.g. Moss and McGowran 1993), and the beds to the upper part of the Buccleuch Formation of the Murray Basin.

Description:

Orientation of the tooth is on the basis of comparison with cheek teeth of *Dorudon* spp., particularly *D. stromeri*, and *Zygorhiza kochii* (see Kellogg 1936) where the anterior edges of asymmetrical teeth tend to be shorter and closer to vertical, and basal cingula are developed on the lingual faces. Insofar as that in *Zygorhiza kochii* only the upper cheek teeth have internal cingula, the Fred's Landing tooth may be considered to be an upper right anterior cheek tooth. However, cingula are too variable in cetaceans to be reliable characters and Fordyce (pers. comm. 19/8/91) has suggested, on the basis of its lack of lingual or posterior recurvature, that the tooth might be a lower left anterior cheek tooth, possibly equivalent to P_2 or P_3 (Fig. 2)

The tooth is not large: its preserved basal length is 16.3 mm, anterior width 8.2 mm, crown height (measured lingually) >16 mm. It is thus slightly larger than the figured tooth (MUGD 1874) of

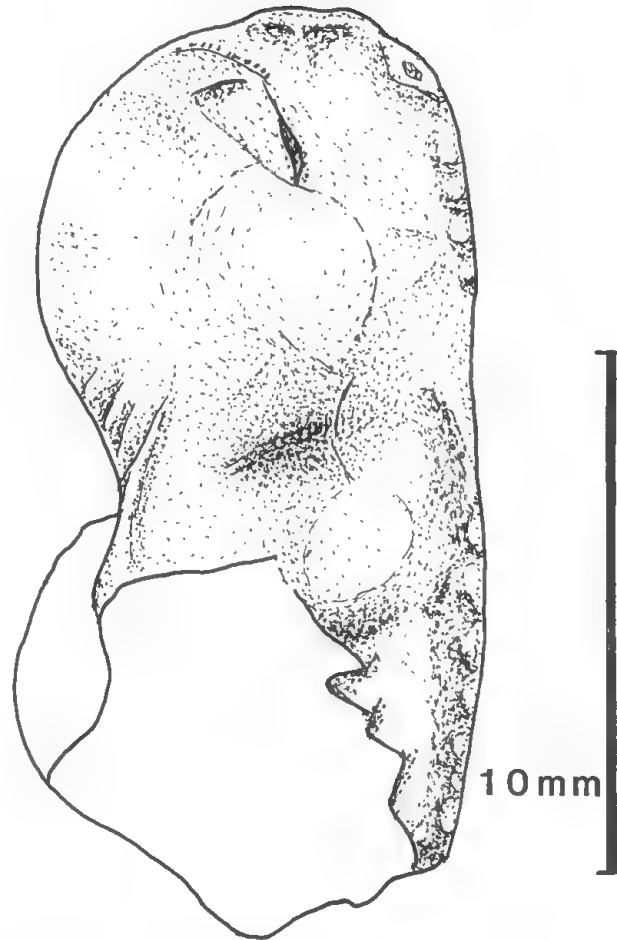


FIGURE 3. Detail of occlusal view. SAM P34517.

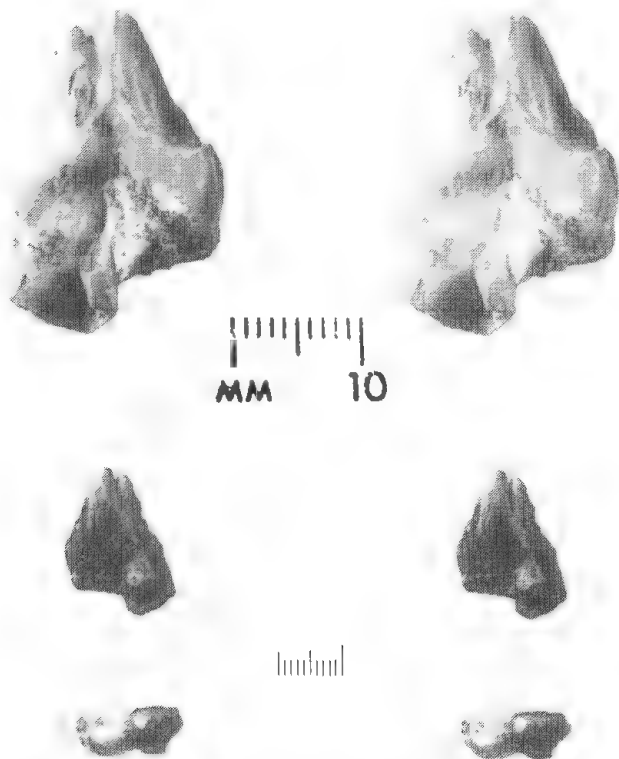


FIGURE 2. Whale tooth SAM P34517, stereopairs in: a, putative lingual b, labial and c, occlusal views. Scale in millimetres.

Mammalodon colliveri (Pritchard 1939). It is also quite high-crowned for its size when compared with other early taxa.

The tooth is damaged posteriorly, probably during life since the enamel edge is rounded and the exposed dentine polished by tooth-on-tooth wear. This has removed the distal cutting edge and all but the uppermost denticle. All denticles show occlusal wear.

The base of the crown rises sharply to its midpoint, corresponding to the indented groove that marks the union of the two roots. (The possibly divided distal end is not preserved.) The apex of the tooth is just anterior to this and is an acute cusp, slightly more convex labially. The anterior edge (carina) descends abruptly forwards to a small denticle about 9 mm above the anterior base of the enamel and continues slightly lingually to a smaller basal denticle (Fig. 3). From here a lingual cingulum curves posteriorly, parallel to the base of the crown, and bears a series of five tiny tubercles which gradually diminish towards the midpoint of the tooth. The tubercles reappear on the posterior half of the cingulum and number at

least six. The cingulum is not continuous across the midpoint of the face. The lingual face of the crown also bears a series of rather coarse, somewhat anastomosing ridges or wrinkles (cristae rugosae) in the enamel of the lower part — only the medial one crosses the cingulum onto the basal zone. The labial face has a slightly greater number of slightly finer ridges which extend higher and lower (to within 2 mm of the base) than on the lingual face. There is no obvious labial (external) cingulum. Of the posterior carina, only the upper-most secondary denticle is preserved (it is about one-third the size of the main cusp) together with the sharp crest joining it to the apex.

Discussion:

The antiquity of this specimen, Early Oligocene, makes it quite significant, since this is when it is considered (e.g. Barnes & Mitchell 1978, Fordyce 1984, 1989) that mysticetes arose from the archaeocetes. Indeed, there are few cetacean specimens recorded of this age and these are listed by Fordyce (1992). Because of its locality, the tooth was initially compared to *Metasqualodon harwoodii* (specimen P8446.4) (Fig. 4b) but that species, although of similar size, lacks any indication of the cingular cusps, and it has a greater cristae density (Pledge & Rothausen 1971). Preservation is also strikingly different, the *Metasqualodon* teeth being black and the new tooth creamy yellow in basic colour, suggesting a different lithologic provenance, and hence formation and age.

The Fred's Landing tooth has been compared with descriptions and figures of those of archaeocetes, particularly species of *Dorudon* (Kellogg 1936, Fordyce 1985), which are much larger than the new specimen. Closest similarity in presumed overall form is seen in *D. stromeri*, e.g. M₁ in Pl. 26 (3h) (Kellogg 1936) and *D. osiris* P² in Pl. 22 (2) (*idem.*). The latter figure shows the teeth in good detail, to indicate that the external face sometimes has a basal cingulum, but in any case does not have cingular tubercles. The greatest similarity of the cingulum and its tubercles is seen in *Zygorhiza kochii*, P² in Pl. 12 (1a) (*idem.*).

There are some similarities with the incomplete premolar tooth from Waihao, New Zealand, referred by Fordyce (1985) to the Dorudontinae. This tooth (ZMT79) is considered to be a second premolar; unfortunately it is broken above the base of the enamel, so it cannot be determined whether a basal cingulum was present. The surface ornamentation of coarse, irregular cristae on the

lingual face and somewhat finer ones on the labial face, together with its overall shape of a steep anterior edge (possibly with a basal denticle) and a posterior edge with at least two large denticles bears a similarity with the new South Australian specimen, which differs most noticeably in its smaller size and lower cristae density.

Comparison with other published cetacean taxa of similar early Oligocene age has proved negative. There is little or no similarity with the possible mysticete from the lower Oligocene of Waikari, North Canterbury, New Zealand (Fordyce 1989), nor with Keyes' (1973) early Oligocene 'proto-squalodontid' from Oamaru, or Mitchell's (1989) *Llanocetus denticrenatus* from the late Eocene/early Oligocene of Seymour Island, Antarctic Peninsula. The later Oligocene cetaceans *Phococetus vasconum* from France, *Platyosphys paulsonii* from the Ukraine, *Sulakocetus dagestanicus* from Caucasus, *Kelloggia barbarus* from Azerbaidzhan, *Aetiocetus cotylaveus* from Oregon, *Squalodon ?serratus* from New Zealand and 'S'. *gambierensis* from South Australia (Emlong 1966, Glaessner 1955, 1972, Mchedlidze 1984) likewise provide no insight into the identity of the Fred's Landing cetacean. This leaves *Metasqualodon* and *Mammalodon* to be considered.

Metasqualodon harwoodii differs slightly from the Fred's Landing tooth (which seems morphologically intermediate between SAM P8446.1 and P8446.4) in being more symmetrical about the main cusp, having finer and more numerous cristae in the enamel, a much less distinct cingulum, and fewer and much smaller tubercles restricted towards the extremities of the cingulum (rather than absent only from the central few millimetres). Fordyce (pers. comm. 19/8/91) doubts that *Metasqualodon* is a squalodontid, and asks if it might not be a mysticete like *Mammalodon*.

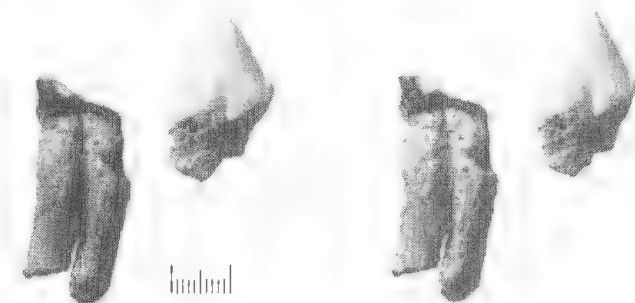


FIGURE 4. Near-contemporary Australian cetacean teeth: a, *Mammalodon colliveri* MUGD1874, b, *Metasqualodon harwoodii* SAM P8446.4 labial (?) views, scale in millimetres.

Comparison with *Mammalodon colliveri* (Pritchard 1939) is frustrating, because of the extremely worn nature of those teeth (Fordyce 1984, Mitchell 1989) (Fig. 4a). However, the isolated tooth MUGD 1874 does show 3–4 small cusps on that part of the lingual cingulum still preserved. That species differs from the Fred's Landing tooth in having more numerous ridges on the labial face of the tooth but the significance of this is unknown. The extreme degree of occlusal wear of the teeth, all in the same plane, is a distinctive feature, which Mitchell (1989) suggested might be related to a particular feeding strategy. In the Fred's Landing tooth, the main cusp is beginning to show signs of wear. Such a character does not seem to occur in the putative squalodontids *Prosqualodon davidis* or *Metasqualodon harwoodii*, although some squalodontids may show it. Fordyce (1982) has compared the skull of *Mammalodon* to that of *Dorudon* spp. and primitive mysticetes, concluding that while there are similarities with the dorudontines, *Mammalodon* is probably a very primitive mysticete. It occupies a morphologically intermediate position but is too recent to have been the ancestor of mysticetes since it is contemporaneous with early cetotheres (Fordyce 1984). *Mammalodon colliveri* is believed to be of latest Oligocene age.

On balance, the greatest similarities of the Fred's Landing tooth seem to be with *Mammalodon colliveri*, yet a case might be made that, on the few characters preserved in these species, it is morphologically intermediate between *Mammalodon* and *Metasqualodon*. The tooth cannot, therefore, be assigned to either taxon,

or indeed to any particular suborder on the material and evidence available.

Genus and species indeterminate, B.

Material:

A right radius, SAM P10875.

Locality:

Cliffs between Port Willunga and Aldinga Bay, South Australia (Fig. 1). Collected by Mr Mark Hagman, 1954.

Age:

It is unfortunate that the locality was not recorded more precisely, since this stretch of coast line encompasses the earliest Oligocene beds (Lindsay 1967, 1985; Lindsay & McGowran 1986) within the Port Willunga Formation. The low dip of the beds (about 3° to the south) means that the bone could be of almost any age within this period. However, it had been thoroughly cleaned and there remained no trace of matrix that might have been used for micropalaeontological examination. On the other hand, the thoroughness of the cleaning suggests the bone came from a sandy or clayey horizon of either the Aldinga or Ruwarang Members of the Port Willunga Formation.

Description:

The bone, kindly identified by R. E. Fordyce (4 February 1981) is a right radius lacking the distal epiphysis (Fig. 5). It is damaged along the whole of the posterior edge, possibly by crushing. The

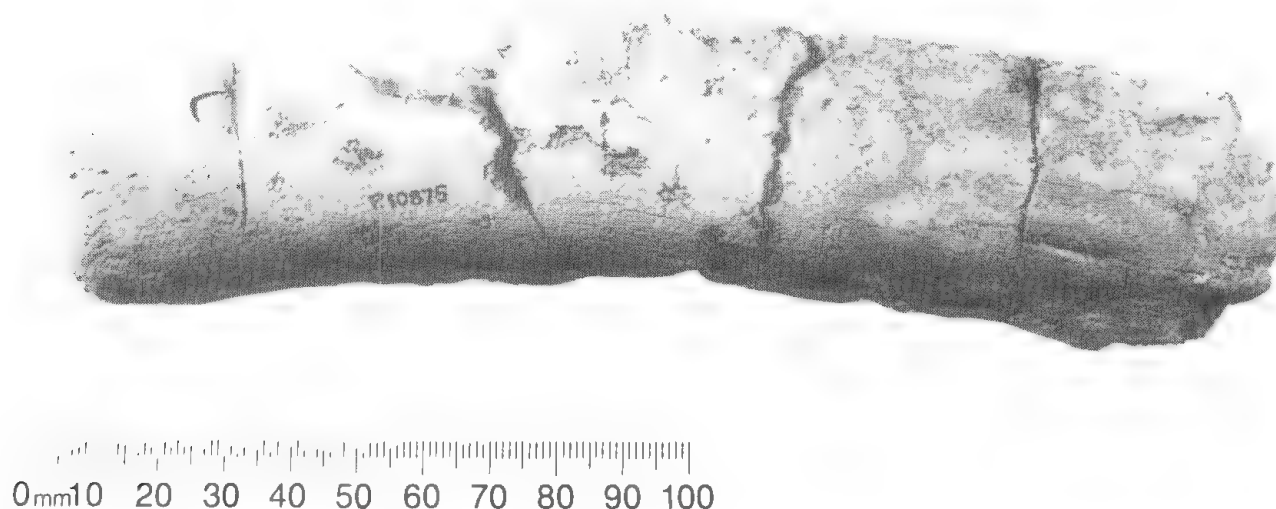


FIGURE 5. Cetacean right radius SAM P10875 from Port Willunga Formation, Aldinga Bay, in lateral aspect. Scale in millimetres.

shaft is slightly curved, convex anteriorly, and more convex on its outer surface. The prominent anterior angle seen in archaeocetes (e.g. Kellogg 1936) has been broken off and only its roots remain. The inner surface of the shaft is almost flat at its midpoint. At the proximal end, the articular surface is ovate to rectangular in outline and slightly concave but is damaged posteriorly, while the distal end of the bone is lenticular in cross-section. The length is 190 mm overall with a midpoint thickness of 22 mm and diameter of more than 42 mm. The proximal end measures 34 mm by an estimated 40 mm while the distal end is approximately 27 x 45 mm.

A diagonal line of punctures can be seen midway along the outer surface of the radius, and can be traced in a tight arc towards the proximal end and back to the posterior edge. These punctures are interpreted as tooth marks, possibly from a small shark, that were inflicted before burial, perhaps even before death, with the attack on the right paddle coming from behind.

Discussion:

The bone shows the pachyostosis typical of *Basilosaurus* (Kellogg 1936) and sirenians. It is straighter and much smaller than the tibia of *Basilosaurus cetoides* (*ibid.*) but resembles it more than it does *Zygorhiza kochii* or *Dorudon* spp., which it slightly exceeds in size. Apart from this only slight curvature of the shaft, the Aldinga bone differs markedly from all these species in the lesser development of the anterior angle. Conversely, its curvature and development of the anterior angle is greater than that seen in some Miocene cetotheres. It is unfortunate that the radius is not preserved in the still-undescribed *Mammalodon* skeleton (Fordyce, pers. comm. 19/8/91), but that would be unlikely to be of great help since the early odontocetes and mysticetes also have archaeocete-like forelimbs (*ibid.*).

CONCLUSIONS

The early Oligocene is seen to be a crucial time in cetacean evolution (e.g. Fordyce 1991, 1992). Despite it being almost impossible to establish its phylogenetic position, it is possible that the Fred's Landing tooth represents, if only morphologically, an intermediate stage between the Eocene (dorudont) archaeocetes and the succeeding mysticetes and odontocetes.

The Eocene/Oligocene boundary period is also important palaeogeographically and palaeoclimatologically, with the establishment of the Circum-Antarctic Current (e.g. McGowran *et al.* 1992; Moss & McGowran 1993; Kennett *et al.* 1975; Fordyce 1977, 1989b, 1992) in the early Oligocene. Fordyce (1992) has linked the start of the radiation of modern cetaceans with this event and its concomitant global cooling and opening of new feeding niches and strategies. The richness and abundance of the planktonic foraminiferal fauna of the Fred's Landing beds suggests a relatively open marine environment (Lablack 1991) which is in agreement with this scenario.

The two specimens reported here, albeit taxonomically and phylogenetically indeterminate, offer the possibility that critical specimens for elucidating the origins of modern whales may eventually be found in this part of the world.

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LATE QUATERNARY CHANGES IN THE MOA FAUNA (AVES ; DINORNITHIFORMES) ON THE WEST COAST OF THE SOUTH ISLAND, NEW ZEALAND

T. H. WORTHY

Summary

The fossil moa faunas from caves on the New Zealand West Coast between Westport and Greymouth are described with particular reference to Madonna Cave. Site stratigraphy and radiocarbon dating of moa bone collagen allow dating of associated faunas. Eight moa species are recorded with a total of 220 individuals. Two distinct moa faunas are recognised : 1. a glacial fauna (10 000 – 25 000 radiocarbon years) consisting of *Pachyornis elephantopus*, *Euryapteryx geranoides*, and a large morph of *Megalapteryx didinus*. 2. a Holocene fauna (0 to 10 000 radiocarbon years) consisting of *Anomalopteryx didiformis* (most common), a small morph of *Megalapteryx didinus*, *Dinornis novaezealandiae*, and *D. struthoides*. Two species, *D. giganteus* and *Pachyornis australis*, were very rare and are not typical components of either fauna in this area.

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T. H. WORTHY, Palaeofaunal Surveys, 43 The Ridgeway, Nelson, New Zealand. Manuscript received 19 April 1993.

Discrete species assemblages of moas associated with specific palaeoenvironments were recognised by Anderson (1989) and Worthy (1990, 1993a). Correlated with environmental change from the Otira Glacial to the Holocene, changes in the species composition of both moa and non-moa faunas were described by Worthy & Mildenhall (1989) and Worthy (1993a), from fossil deposits in Honeycomb Hill Cave, Oparara Valley, Northwest Nelson. It is reasonable to expect that such changes would have parallels in all areas of New Zealand where significant vegetation changes occurred between glacial and interglacial conditions.

In many continental areas palaeobiogeography of mammals has been used to infer climate, for example late Pleistocene changes in Australia (Lundelius 1983), but only recently has the use of birds been advocated (Baird 1989). Baird argues that birds are better suited for palaeo-environmental reconstructions because they are well represented in the fossil record, can be identified to species level often, and identification of niche in modern analogues is easier. Baird (1991) considered the fossil bird assemblages in several sites to be indicative of past environmental conditions, and with radiocarbon dating, documented environmental change through the late Pleistocene that was consistent with patterns obtained by other means.

New Zealand has a large body of data which indicates it had a similar pattern of vegetation change to Australia. These vegetation changes are

correlated with climatic changes during the interglacial – glacial cycles (McGlone 1985, 1988). As the fossil record within New Zealand caves is only known to extend from the Otira (last) Glaciation to the present, this is the period considered here. Palynological studies show that the majority of sites in the South Island were dominated by grassland and shrubland taxa, with trees less than 10% of total taxa indicating that forest was sparsely present, if at all, in many regions during the glacial maximum (22 000 – 14 000 years ago) (McGlone 1988). The climate then was characterised by temperatures about 5 °C cooler and by being considerably drier, a combination which effectively excluded forests. During the late glacial (14 000 – 10 000 years ago) pollen evidence suggests rapid afforestation occurred in many areas, at slightly different times depending on local conditions. For example, around Wellington reafforestation was much later than elsewhere (Lewis and Mildenhall 1985), perhaps a corollary of the present frequent exposure to southerly winds there now. In many South Island areas the late glacial saw grasslands give way to shrublands and tall scrublands. These changes were correlated with increased temperatures and increased precipitation. At the commencement of the Holocene (10 000 years ago) a return to present day temperatures and precipitation similar to that now resulted in rapid widespread vegetation change with tall podocarp forests becoming dominant in most lowland areas (McGlone 1988).

New Zealand cave fossil deposits, unlike most swamp and all dune deposits, range in age from the Otira Glacial to the present so, alone, have potential for demonstrating faunal changes correlated with the above described vegetation changes. Demonstration of these faunal changes is conditional on investigation design. If a cave is considered to be the 'site' and all fossils indiscriminately associated together, or all faunas from caves within a region considered as one, then by investigation design, perception of temporal changes is ruled out. Dating is necessary to determine the time span of deposition for each discrete site in a cave. In this regard isolated skeletons, or bones in surface deposits within a cave, should be considered as discrete events which need to be individually dated, unless on the basis of sedimentary history within the cave, or similar speleogenetic evidence, an upper age limit can be set on fossil deposition.

The following example illustrates how study design compromises resultant conclusions. Atkinson & Millener (1991) analysed the cave fossil fauna around Waitomo in the North Island using data compiled from sites in 156 separate caves (Millener 1981), not 37 as they stated. Insufficient attention was paid to the age of the fossils. Most were collected by amateurs from surface deposits that could have been up to 100 000 years old (speleothems of this age are known in some Waitomo caves (Hendy 1969)). Younger fossils were more likely to have been more abundant for two reasons. Firstly, younger fossils would have been subject to destructive processes for a shorter period of time, and secondly in many cases younger sediments overlie and therefore obscure older material. No attempt was made by these authors to justify temporal association of fossils from individual sites within caves – caves were treated as sites – nor was temporal association of deposits from separate caves proven, beyond the observation that dates for fossils from 10 caves ranged from one to twenty five thousand years old. Despite the proven age of the fossil deposits spanning two major climate regimes, all species in the faunal list were assumed to have been present contemporaneously between 6 000 and 1 000 years BP. To treat all fossils as a unit necessarily obscured any patterns there may have been and so, as younger fossils predominated, Atkinson and Millener's approach resulted in the conclusion: 'A humid lowland forest thus dominated the area throughout the period when faunal remains were accumulating'. This is a description of the environment that

prevailed in the area during the Holocene, and describes conditions that must have differed from those prevailing during the glacial period, if the palaeotemperature curve for the region is any indication (Hendy 1969).

Apart from age, the limitations imposed by taphonomic processes (Baird 1991), especially as they apply to species representation, need to be understood and assessed before sites are compared. With increased water flow at a site there is progressive removal and destruction from smaller to larger fossils resulting in a marked bias towards preservation of moa bones in stream sediments. The New Zealand birds observed to be specific indicator species of open-country habitat, for example the pipit and New Zealand quail, have small bones for which suitable preservation conditions are rarely encountered in New Zealand caves. Their absence or rarity in the Waitomo fauna as a whole (as so far described) does not preclude their having been common in the area during the Otiran.

The present study arose out of a survey of the Quaternary fossil bird fauna of the Punakaiki karst region, West Coast, South Island (Worthy & Holdaway 1993). Preliminary examination of the Canterbury Museum's collection of fossils from the region indicated that elements of both the *Anomalopteryx* and *Euryapteryx* assemblages of

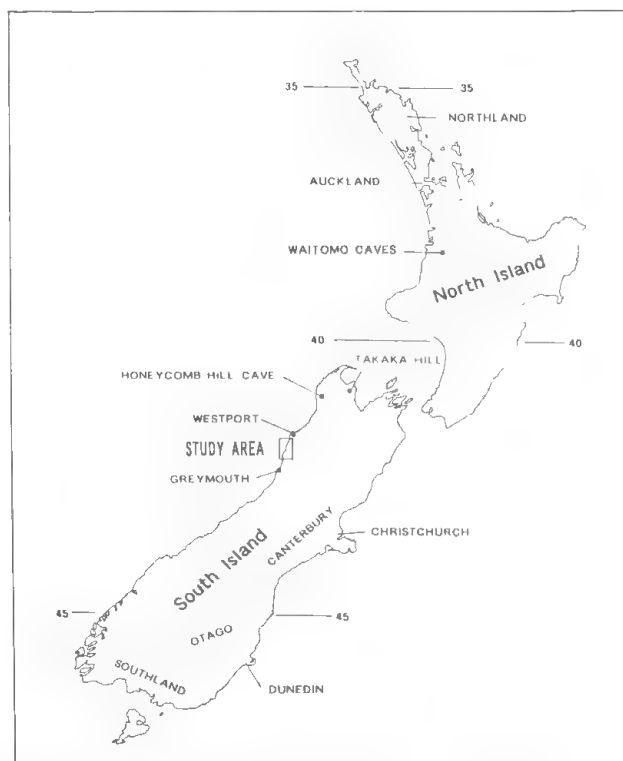


FIGURE 1. Locality map showing the study area in New Zealand.

RESULTS

Fossil Deposits

The fossil sites located within Madonna Cave are shown on Figure 2. There were three main types of fossil deposits in the cave: 1. Allochthonous deposits of scattered water-

transported fossils that were not enclosed in sediments (sites 1-9,14,15); 2. Allochthonous deposits of fossils that were in fluvial sediments (sites 11,11a,13,16); 3. Fossils that had accumulated in autochthonous deposits below entrance shafts or lay, as individual skeletons, near an entrance. Limited water transport (2-10 m) of some fossils had occurred at some sites, for example The Morgue. (sites 10,12,13a,17,18,19).

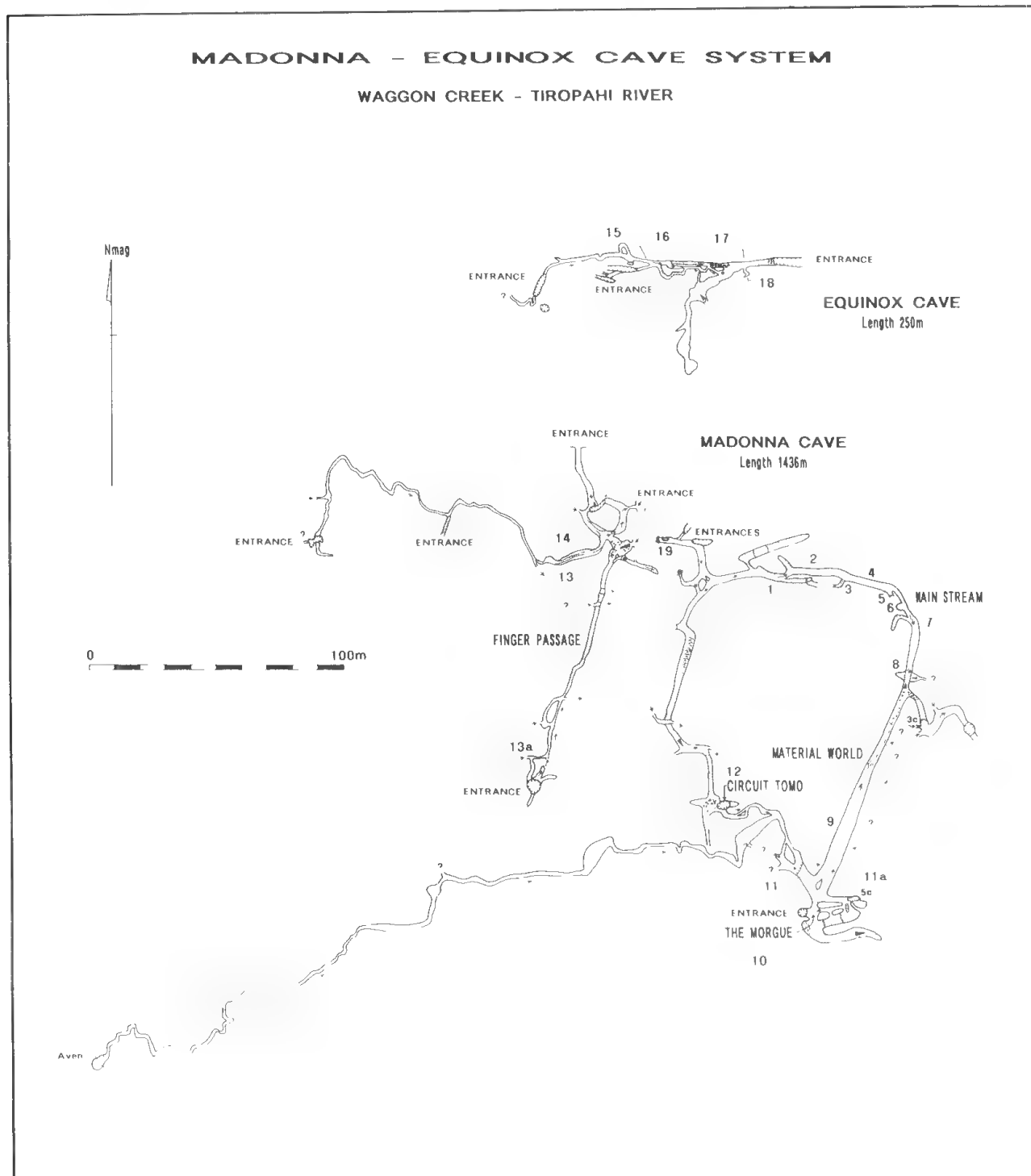


FIGURE 2. Map of the Madonna: Equinox Cave System showing the location of fossil sites 1-19 referred to in the text.

Anderson (1989) occurred in apparent geographic sympatry which would have been inconsistent with observations made by Worthy (1990). Further north at Honeycomb Hill Cave on the West Coast recent research has shown that moa assemblages changed with climate from the Otiran to the Holocene (Worthy & Mildenhall 1989; Worthy 1993a). I therefore thought it probable that the fossil deposits of the Punakaiki area also preserved elements of at least two successive and distinct moa faunas.

During the survey of caves in the Punakaiki area a site was searched for in which to test the hypothesis of moa faunal turn-over. I chose Madonna Cave because it contained several closely associated sites, each with stratigraphic control, and large numbers of fossils. The initial examination of the cave revealed a number of rich and discrete fossil sites representing a range of depositional environments. Some were in fluvial stratified sediments, and others under entrances. Different species assemblages were noted in different sites. In addition, it was noted that discrete periods of sedimentation had incorporated fossils in stratified sediments that were therefore likely to provide dates reliable for building a chronology of change in moa species. Later erosion had re-excavated most of these sediments leaving only remnant banks, and because these fluvial sediments had also been deposited and eroded from passages beneath entrance shafts, the fossil deposits under the shafts must have accumulated subsequent to the erosion. Therefore, data from these various sites could be used, in combination, to test the hypothesis.

Madonna Cave is between Waggon Creek and Doubtful Creek on the south side of the Tiropahi (Four Mile) River, between Westport and Greymouth (Fig. 1). The approximate grid reference for the centre of the cave system, on the metric 1: 50 000 map series NZMS 260, is K30 819127. The cave system drains a karst area, about 200 m above sea level, that has many dolines and natural traps in the form of shafts and grikes. The area is vegetated in mature mixed beech/podocarp forest with emergent rata trees up to 35 m in height. The forest floor and tree trunks are cloaked in deep moss that is indicative of the regular high rainfall (c. 3 000mm).

The cave system comprises three sections: Equinox Cave about 250 m long; and the 'upper levels' and the 'lower levels' of Madonna Cave which together have 1 436 m of surveyed passages in them. The cave is characterised by numerous entrances (see Fig. 2). In each area of the cave

small streams now flow in the lowest levels but it is in the older stream courses at higher levels that sedimentary deposits are preserved. These sediments vary from sands to coarse gravel and moa fossils are visible in some. Abundant moa fossils also occurred in the streambeds.

DEFINITIONS

Allochthonous versus autochthonous. Fossils in caves have been classified as allochthonous (died at a different place to that in which the fossils are deposited), or autochthonous (where the fossils are found at or near where the animals died) by Baird (1991). In the surface environment such an assessment of fossil sites prior to palaeoenvironmental reconstruction is extremely important as fossils in fluvial deposition sites could have their origin many miles away, and therefore could have been transported out of the environment they lived in. Assessing cave sites in this fashion would result in fossils from stream sediments being classed as allochthonous. However, I contend that to discount use of data from these sources for palaeoenvironmental reconstruction, as is necessary for surface sites, would omit relevant data. This view is held as in the majority of caves, and especially within Madonna Cave, all fossiliferous fluvial sediments can be easily traced to their point of origin that is at most only a few hundred metres distant. So all bird fossils in such cave sediments can be considered autochthonous with respect to the home range of the living bird, and can justifiably be used in palaeoenvironmental reconstructions. I therefore use the terms 'allochthonous deposits' and 'autochthonous deposits' to indicate only that bones have, or have not, been secondarily transported from the point of death. I use the term 'autochthonous assemblage' to indicate that it is an assemblage of local derivation, which may be in either of the above deposit types.

MNI is minimum number of individuals determined from the number of the most abundant ipsolateral element.

Radiocarbon dating was done by the Institute of Geological and Nuclear Sciences Ltd laboratories at Lower Hutt, New Zealand, on the collagen fraction of bones, and ages are given as 'conventional radiocarbon age', where Libby $T_{1/2}$ = 5568 yrs BP.

MNZ is the Museum of New Zealand Te Papa Tongarewa (was the National Museum of NZ) Wellington.

1. Water transported fossils.

Main Stream. Fossils at sites 1–8 were found in allochthonous deposits as isolated bones in the floor of the streambed. After recording all fossils it was decided that generally only femora would be collected leaving other fossils *in situ* for future cave visitors to see. The fossils collected represented all species and the maximum number of individuals present in sites 1–8 (MNZ S28055–28065) (Table 1). The exception to the policy of collecting femora was in site 8 where a tarsometatarsus of *Pachyornis* (S28064) was collected since this taxon was otherwise unrepresented. The majority of fossils were little worn and were whole bones, but at the most downstream part of the stream (site 8) a few very worn fragmentary bones of species not otherwise represented in the fauna were found. These included a distal left femur and a distal left tibiotarsus of *Pachyornis* and a distal right tarsometatarsus of *E. geranoides*.

The age of the majority of fossils in sites 1–8 was considered likely to be Holocene with the few worn specimens (detailed above) interpreted as probably reworked from older sediments. One bone of *A. didiformis* K30/f62b (assumed 'young'), and another, part of *P. elephantopus* S28064, K30/f62a, (assumed 'old') were dated to test this (Table 2).

Near site 1 a small side-passage on the true right had several fossil moa bones scattered along its terminal crawlway. These were not collected and were considered to be a sub-sample of the fauna in the main stream sites 1–8. Bones of

Dinornis novaezealandiae and *Anomalopteryx didiformis* were seen.

Fossils at sites 14 and 15 lay in the bed of the stream. Both sites were similar in that they were about 10 m above the Main Stream in passages whose sediment banks had a different sequence of sediments to that seen in the Main Stream. I interpreted this to mean that the passage around sites 14 and 15 had escaped the last period of sedimentary infill and re-excavation that the Main Stream had been subjected to. As the small streams in these passages come from shaft entrances it was postulated that moas of both Holocene and pre-Holocene derivation could be present. All specifically recognisable bones were collected from site 14 and a *Pachyornis elephantopus* bone, chosen because this taxon was not present in the assumed young sites 10 and 12, was dated. Fossils found in the stream bed at site 15 were left as reference specimens.

2. Fossils enclosed in fluvial sediments

All along the Main Stream there were remnant banks of sediment reflecting an earlier period of sedimentation followed by erosion. Near site 8 two bones were observed apparently *in situ* near the top of the sediment bank: one an *Anomalopteryx didiformis* femur was left *in situ*, and the other, a femur of a juvenile *Dinornis* MNZ S28218, was collected. Opposite where the stream sinks another fossil (MNZ S28079), of undetermined moa species, was collected from about 0.5 m below the top of the sediments. Because these sediments

TABLE 1. The identity of 63 moas represented in collections from Madonna Cave, or by *in situ* material, and their distribution within sites is summarised here. Specimens marked * represent individuals known from *in situ* material only. All the rest are represented by collected specimens that were chosen to represent the total material from the site and so MNI at each site would not increase with further collecting even though many bones remain.

Site	<i>A. did.</i>	<i>M. did.</i>	<i>D. str.</i>	<i>D. nov.</i>	<i>D. gig.</i>	<i>E. ger.</i>	<i>P. ele.</i>
1–8	6	0	2	2	0	1*	1
9	0	3	1	0	0	0	0
10	5	5	2	8	1	0	0
11	0	1	0	0	0	0	3
12	3	1	1	1*	0	0	0
13	0	1	0	0	0	1	1
13a	1	0	0	0	0	0	0
14	3	0	1	0	0	0	1
15	0	0	0	1*	0	0	1*
16	0	0	0	0	0	2	1
17	0	0	0	1*	0	0	0
19	1*	0	0	0	0	0	0
Total	19	11	7	13	1	4	8

border an active stream and are no more than 0.5 m above the normal water level they are probably considerably younger than those hereafter described.

Site 11. This site was at the south end of Material World. The limestone floor of the passage was visible at the end of this passage but remnant sediment banks extended to the roof on both sides. At site 11 the sedimentary sequence was as follows: about 0.5 m of stream gravels and sands rested on the limestone floor. The gravels were overlain by a 0.5 m thick layer of slightly rounded limestone cobbles embedded in sand which was, in turn, overlain by homogenous sands that filled the 0.2–0.3 m space between the cobble layer and the roof. Immediately west of site 11, a 2 m bank overhung a streamway, but the passage leading upstream via the crawl (see map), preserved the sequence of sediments very well. Also, half way up the passage towards Circuit Tomo, an alcove preserved the same sedimentary sequence. There the available roof space above the cobbles was much greater and the sand layer much thicker. Immediately east of The Morgue the passage roof was also much higher and the sedimentary sequence was preserved in several places showing the sand layer was at least 3 m thick. Fossils were found at the interface of the sand and cobble layers: two bones (MNZ S28076, S28080) at site 11, and one at site 11a that was left *in situ*. Two fossils (MNZ S28077–8) were recovered from the crawl immediately west of site 11. Although not *in situ* preservation characteristics and adherent matrix indicated they had been dislodged from the same layer. Part of the *M. didinus* femur collected from *in situ* in site 11 was dated.

Site 13. Stream laid sand and gravel banks

indicated that this area of the cave had been infilled to the roof. Worn fossil bones from single individuals of *Megalapteryx* MNZ S28082, *Pachyornis* MNZ S28081 and *Euryapteryx* MNZ S28083 were scattered on the surface of the floor formed on the eroded surface of these sediments. In one of the remnant banks of sediment lining the site, *in situ* fossils from these individuals were recovered, indicating that those fossils on the surface had been eroded from the sediments. One of the eroded *Euryapteryx* bones recovered from the surface of this site was dated.

Site 16. Here exactly the same sequence of sediments as seen at site 11 was preserved. Some fossils (MNZ S28121) were exposed on the surface but excavation revealed that other fossils were deposited on top of the limestone cobble layer (MNZ S28220–223). Several were found embedded in sand adjacent the upstream end of a large fallen rock where the stream had apparently washed them. About one metre 'upstream' of this rock, a remnant bank of sediment overlying the cobbles was found to contain an articulated series of moa vertebrae MNZ S28224 at a depth of three to four centimetres and about 30 cm above the sand cobble interface. These are most probably the surviving parts of the skeleton otherwise represented by S28121. This skeleton was deposited near the end of the deposition period as a whole carcass. The femur of S28121 was dated to provide a minimum age for the site and the more deeply buried disarticulated material.

3. Fossils accumulated near entrances

The most significant site was The Morgue, site

TABLE 2. Radiocarbon dating results from Madonna Cave. Specimens are identified by species, site of origin, Fossil Record Number FRN, and the laboratory sample number NZA (Accelerator mass spectrometry laboratory) or NZ (Gas counting laboratory).

Site	Species	FRN	NZA or NZ ¹	Radiocarbon age
8	<i>P. elephantopus</i>	K30/f62a	2505	14740±110
8	<i>A. didiformis</i>	K30/f62b	2443	2197±86
10	<i>A. didiformis</i>	K30/f65a	2506	5447±87
10	<i>D. novaezealandiae</i>	K30/f65b	7925 ¹	5893±88
10	<i>D. giganteus</i>	K30/f65c	7926 ¹	2829±75
10	<i>M. didinus</i>	K30/f65d	2503	782±83
11	<i>M. didinus</i>	K30/f67	2780	13150±140
12	<i>A. didiformis</i>	K30/f66	2521	1076±83
13	<i>E. geranoides</i>	K30/f63	2779	11090±100
14	<i>P. elephantopus</i>	K30/f64	2446	20680±160
16	<i>E. geranoides</i>	K30/f61	2445	23780±210

10. Here an entrance shaft at least 15 m deep was the natural trap that had accumulated a large amount of material in an autochthonous deposit. The history of sedimentation in the adjacent passages was one of deposition, wherein the sequence recorded for site 11 was deposited, followed by erosion right back to floor level to leave only sediment remnants along some walls and in alcoves. Only following this erosion event could the fossils observed at The Morgue have started to accumulate, and therefore they must all be younger than those seen in site 11. The base of the entrance shaft intersects a passage aligned approximately north-south which, either side, is only 0.5 m high. The water that formed the shaft now drains via a 20–30 cm high bedding-plane passage to the east. Although impenetrable this bedding can be approached via a small passage from the east that starts at the top of a 5 m drop, below which the water ultimately sinks away in gravels. Fossils were mostly collected from the base of the entrance shaft and from the bedding plane passage and its downstream outlet (MNZ S28088–28112, 28114–28120). Articulated remains of one subadult *Dinornis novaezealandiae* and one *Anomalopteryx didiformis* were found in the passage to the south indicating that these trapped birds had passed the low passage in this direction. Immediately north of the base of the entrance shaft an articulated skeleton of *A. didiformis* was left *in situ*. Fossils found at site 9 scattered along the floor of Material World are interpreted as remains of birds that were trapped by the Morgue entrance and passed the low passage to the north. It is significant that these are mainly from 3 individuals of *Megalapteryx*, the smallest moas in the region (MNZ S28067–28071). These small *M. didinus*, like others in site 10, are a small morph of the species identified by Worthy & Holdaway (1993) as only present in Holocene deposits in the area. One specimen in site 9 was a very worn, possibly reworked, femur of *Dinornis* (MNZ S28066). Four bones were dated from site 10, one from each of the following taxa: *Megalapteryx didinus*, *Anomalopteryx didiformis*, *Dinornis novaezealandiae*, and *D. giganteus* (from S28114).

Circuit Tomo: site 12. This site was at the base of another shaft entrance. Fossils were located in an autochthonous deposit of rockfall debris at the shaft base or scattered down the first few metres of the stream passage away from the shaft. Sediment banks with the same stratification as sediments preserved at site 11 indicate that fossils in site 12 had the same potential age range as

those in site 10, and had to be younger than those in site 11. The *M. didinus* specimen was one of the small morphs of the species.

Other sites. A few fossils were recovered from site 13a. Bones of an individual *A. didiformis* were left *in situ* near the upstream entrance to the Main Stream (site 19). In Equinox Cave at site 17 a complete *D. novaezealandiae* skeleton was left *in situ* lying on the surface, and is necessarily younger than the fossils enclosed in sediments nearby at site 16. Closer to the entrance a small crawlway leads off and it contained some fossils, but none of moas.

Summary of Moa Distribution in Madonna Cave

Table 1 lists the individual sites described above and the moas, by species, from each of them: 63 individual moa are represented in the total collection. The geological ages for each site are indicated from the dates listed in Table 2. Sites 11, 14 and 16 are exclusively Otiran in age and contain *Pachyornis*, *Euryapteryx*, and *Megalapteryx*. Sites 10 and 12 are exclusively Holocene, and have *Anomalopteryx*, three *Dinornis* species with *D. novaezealandiae* the most abundant, and *Megalapteryx*. From the cave's sedimentary history site 9 should be associated with 10 and 12, and so is of Holocene age. Three dates were obtained from fossils found loose in streambeds; one from site 15, and two from the Main Stream sites 1–8. In the Main Stream the *Anomalopteryx* was late Holocene and in the *Pachyornis* Otiran. In site 15 the *Pachyornis* bone that was dated was Otiran in age.

DISCUSSION

Allochthonous and autochthonous deposits in Madonna Cave contain fossils of various ages that can be regarded as autochthonous assemblages, that because of known age ranges provide useful palaeoenvironmental indicators. Deposits beneath shafts from the surface contain only Holocene faunas, fluvial sediments not in active streamways contain Otiran faunas, and streamways contain mixed Otiran and Holocene faunas. Holocene faunas were characterised by abundant *Anomalopteryx didiformis*, *Dinornis novaezealandiae*, *D. struthoides*, and small to medium morphs of *Megalapteryx didinus*. The

Otiran fauna contained no *A. didiformis*, but common *Pachyornis elephantopus* and *Euryapteryx geranoides*, with *M. didinus* as a medium to large morph only.

Local comparisons

A series of dates was obtained from moa bones from Te Ana Titi (Worthy & Holdaway 1993). The single *Pachyornis australis* individual was Otiran in age, and the *Dinornis novaezealandiae* of Holocene age. The 18 *Megalapteryx didinus* recorded from Te Ana Titi ranged from the largest ever recorded to nearly the smallest. The dates obtained by Worthy & Holdaway (1993) clearly showed that all the largest, without exception, were of Otiran age and the smallest, of Holocene age. These data support the hypothesis of post-glacial dwarfing proposed by Worthy (1988). It is therefore significant to note that the *Megalapteryx* recorded from the Holocene sites 9, 10 and 12 in Madonna were all small individuals.

Table 3 lists all moa individuals recorded from the Punakaiki karst area by Worthy & Holdaway (1993) regardless of specimen age. *A. didiformis* was the most abundant, with nearly twice the number of the next most frequently recorded species. This reflects the preponderance of Holocene sites and that this species was the most common in them. *Megalapteryx didinus*, the only species occurring in both Otiran and Holocene deposits, was the next most frequently encountered. *Dinornis struthoides* and *D. novaezealandiae*, the remaining common Holocene species were the next most abundant. The Otiran *Pachyornis* and *Euryapteryx* occurred in lower frequencies consistent with there being

fewer surviving Otiran sites. *P. australis* and *D. giganteus* were very rare, and so in the Punakaiki karst were considered to have been outside of their preferred geographic ranges.

Comparison with other areas

The only place where comparable data has been obtained is Honeycomb Hill Cave System in the Oparara Valley, northwest Nelson. This area ranges in altitude from 200 – 300 m a.s.l.. There the Otiran moa fauna was dominated by *Pachyornis elephantopus*, *P. australis* and *Megalapteryx didinus*. *Euryapteryx geranoides* was extremely rare (one individual among hundreds), and *Dinornis novaezealandiae* and *D. struthoides* were both rare. In the Holocene *Pachyornis* and *Euryapteryx* were not recorded and *Anomalopteryx didiformis* dominated with *D. novaezealandiae* becoming more common (Worthy & Mildenhall 1989, Worthy 1993a). Data documenting changes in moa fauna over time have not been published for any other area.

Worthy (1990) described the 'Holocene' moa faunas for many regions in New Zealand. The Holocene faunas of western South Island, as shown by Honeycomb Hill Cave and the Punakaiki karst, were similar to those in lowland wet forest areas in Southland, and central, western areas of the North Island with *Anomalopteryx didiformis* and *Dinornis novaezealandiae* dominating in both. The Otiran faunas of the western South Island were most like the Holocene faunas of eastern areas of the South Island but there were significant differences. As seen above, in the west, *Megalapteryx didinus* accompanied *Pachyornis elephantopus* and *Euryapteryx*

TABLE 3. Summary of total numbers of moa individuals recorded from the Punakaiki karst area by Worthy & Holdaway (1993). MNI in coll. is minimum number of individuals determined from specimens in museum collections (some of which are voucher specimens for more material in the fossil site). MNI in situ refers to those recorded from the cave site only, and for which no voucher specimen was collected.

Dinornithiformes	MNI in coll.	MNI in situ	Total No.	(%)
<i>Anomalopteryx didiformis</i>	75	6	81	(40.3)
<i>Megalapteryx didinus</i>	28	10	38	(18.9)
<i>Pachyornis elephantopus</i>	11		11	(5.5)
<i>Pachyornis australis</i>	3		3	(1.5)
<i>Euryapteryx geranoides</i>	17		17	(8.4)
<i>Dinornis struthoides</i>	24	1	25	(12.4)
<i>Dinornis novaezealandiae</i>	22	2	24	(11.9)
<i>Dinornis giganteus</i>	2		2	(1.0)
TOTAL	182	19	201	

geranoides, but in the east, although the latter two species were common, they were accompanied by *Emeus crassus* (unknown in the west) and *D. giganteus* (very rare in the west).

The western Otiran fauna was more similar to that in Otiran loess deposits in eastern South Island where *Pachyornis elephantopus* dominated with *Euryapteryx geranoides* the next most abundant species. *A. didiformis*, *M. didinus*, and *D. novaezealandiae* were not present and *E. crassus*, *D. giganteus* and *D. struthoides* were rare (Worthy 1993b). On Takaka Hill in northwest Nelson the Otiran fauna consisted of rare *M. didinus*, and common *Pachyornis elephantopus*, *P. australis* and *E. geranoides* (Worthy unpubl. data).

The western distribution of moas in their dated context support previous notions of habitat preference of individual species (Worthy 1990). The mainly western distribution of *M. didinus* in both Otiran and Holocene periods suggests that it preferred wetter and cooler habitats. Generally it was an upland bird of the montane forests to the subalpine zone (Worthy 1988, 1989b). However, in the Holocene forests of the Punakaiki area, the only known lowland population of *M. didinus* was represented by a race where individuals were smaller than *Anomalopteryx* and their upland counterparts. It is possible that the small size of individuals enabled this population to avoid competition with *A. didiformis* which was the only other emeid present. Elsewhere populations of these two species met in ecotones in the montane forest zone and were separated by altitude (Worthy 1990). *P. australis* was rare in both time periods in Punakaiki. An abundance in Otiran Honeycomb Hill Cave and Takaka deposits compared to its presence mainly in subalpine deposits during the Holocene indicate that it was an upland species (Worthy 1989a, 1989b). In contrast *P. elephantopus* and *E. geranoides* were both common during the Otiran in a range of areas, including lowland eastern areas and western sites from sea-level to 700 m, but during the Holocene were only in eastern dry lowland areas. These

observations support the hypothesis that these taxa preferred relatively openly vegetated areas where mosaics of grass and shrubland dominated the vegetation.

CONCLUSION

The data presented here clearly show that there were marked changes in distribution of moa species on the West Coast of the South Island between the last Glacial period and the Holocene. Usually only 3 to 4 species co-existed at one time and so moa species assemblages could be used as stratigraphic indicators. The presence of *E. geranoides* and *P. elephantopus* are indicative of Otiran age deposits and *A. didiformis* and *D. novaezealandiae* Holocene deposits. In addition to changes in species distribution *M. didinus* exhibited marked post-glacial dwarfing. The smallest and largest forms (defined Figure 26, Worthy & Holdaway 1993) are therefore useful stratigraphic indicators for the Holocene and Otiran periods respectively. The national implication of these data is that faunas from different sites should not be amalgamated into a regional fauna and analysed as a unit without reference to temporal variation unless temporal association is first proven. Cave systems throughout New Zealand can be expected to have superimposed Otiran and Holocene faunas and only careful study of stratigraphy combined with dating will separate them.

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AN EXTINCT SPECIES OF CORMORANT (PHALACROCORACIDAE, AVES) FROM A WESTERN AUSTRALIAN PEAT SWAMP

G. F. VAN TETS

Summary

Microcarbo serventyorum n.sp. is described from a pelvis with proximal parts of the femora and some caudal vertebrae, which were found in a peat swamp at West Bullsbrook, north of Perth, Western Australia. Age is not known, but is probably Holocene. These bone exaggerated the pelvic differences between those of small extant species of *Phalacrocorax* and *Microcarbo* and are therefore included as a new species in the latter genus. Presumably *M. seventyorum* was able to forage in even more confined waters than other species of *Microcarbo*.

AN EXTINCT NEW SPECIES OF CORMORANT (PHALACROCORACIDAE, AVES) FROM A WESTERN AUSTRALIAN PEAT SWAMP

G. F. VAN TETS

VAN TETS, G. F. 1994. An extinct new species of cormorant (Phalacrocoracidae, Aves) from a Western Australian peat swamp. *Rec. S. Aust. Mus.* 27(2): 135–138.

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G. F. van Tets, Wildlife & Ecology, CSIRO, P.O. Box 84, Lynham, Australian Capital Territory 2602 and Division of Archaeology and Natural History, Research School of Pacific and Asian Studies, Australian National University, Australian Capital Territory 0200. Manuscript received 13 April 1993.

At the 16th International Ornithological Congress in Canberra, I postulated that Australasia might be the main centre of generic and sub-generic divergence of the extant Phalacrocoracidae (van Tets 1976). Since then Siegel-Causey (1988) raised my generic separation of cormorants, *Phalacrocorax* versus shags, *Leucocarbo* to that of the subfamilies Phalacrocoracinae and Leucocarbininae. I agree with these subfamilies (van Tets pp. 808–809 in Marchant & Higgins 1990), but disagree with some of Siegel-Causey's generic and specific arrangements in those subfamilies. In particular I accept as cormorants in the Phalacrocoracinae only *Microcarbo* and *Phalacrocorax* including the sub-genus *Hypoleucos*.

Evidence for a new extinct Australian species of cormorant is provided by a pelvis with proximal parts of the femora and some caudal vertebrae (Figs 1–4). They were found 9 January 1970 in a peat swamp at mining lease 19H 'Melaleuca', West Bullsbrook, at 30 km north of Perth, Western Australia (31°41'S 115°59'E). They were noticed on a stockpile, before loading on to a truck, but after rotation and blading, from an estimated depth of about one foot (=0.3 m). Age is not known, but is probably late Holocene. C. Mizen forwarded it per A. R. Burns to Duncan Merrilees at the Western Australian Museum, who registered it 12 February 1970 as WAM 70.2.10.

WAM 70.2.10 was compared with a wide range of material in the collections of the Australian Museum (AM) Sydney, the Australian National Wildlife Collection (ANWC) CSIRO Canberra and the University of Michigan Museum of

Zoology (UMMZ) Ann Arbor. The material included all families and genera of Pelecaniformes and most species of Phalacrocoracidae including all of *Microcarbo* (*sensu* van Tets 1976).

SYSTEMATICS

In penguins (Spheniscidae), darters (Anhingidae), cormorants and shags (Phalacrocoracidae), the cranial facet of the pelvis is convex and not concave as in frigatebirds (Fregatidae), gannets and boobies (Sulidae), nor saddle-shaped as in pelicans (Pelecanidae), tropicbirds (Phaethontidae) and in almost all other kinds of birds.

The pelves of the Spheniscidae differ from those of the Anhingidae and Phalacrocoracidae by having a fenestrated preacetabular ala of the ilium and lacking ventral spines (van Tets & O'Connor 1983). On the pelves of the Anhingidae prominent ilial crests flank the median dorsal ridge and shield (Olson 1975) and on those of the Phalacrocoracidae only the caudal half of the shield. In the shield there are up to six pairs of postacetabular foramina in Anhingidae and up to eight in Phalacrocoracidae. These foramina are relatively smaller in Anhingidae than in Phalacrocoracidae.

On the femur, the trochanter is about as tall as the head in Phalacrocoracidae and not lower as in WAM 70.2.10, Anhingidae and Sulidae (van Tets *et al.* 1989).

On the ilia lateral to the first pair of postacetabular foramina is a pair of rough

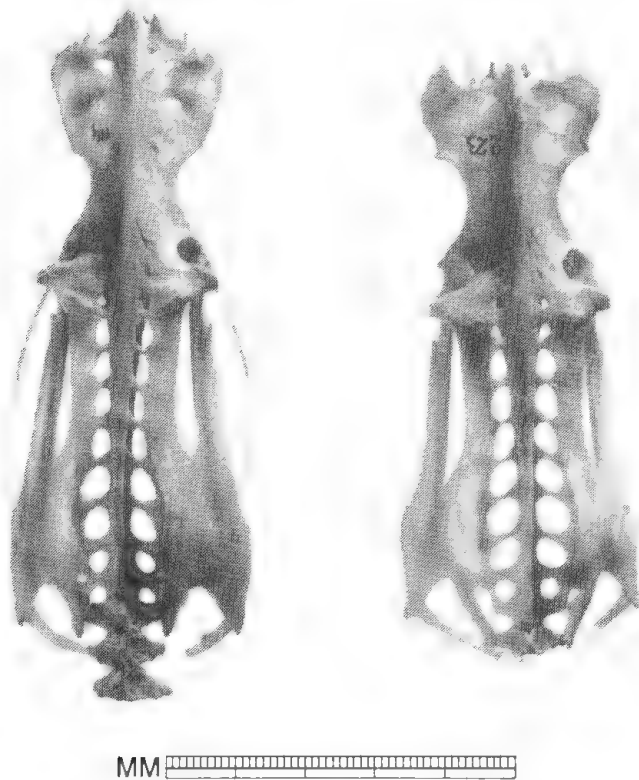


FIGURE 1. Dorsal view of pelvis. Left: *Phalacrocorax sulcirostris* ANWC BS-1310. Right: *Microcarbo melanoleucos* ANWC BS-1419.

irregular 'facets', which are about as wide as broad in *Phalacrocoracinae* and are longer than broad extending alongside the second pair of foramina in *Leucocarbinae*, but are variable and intermediate in the Pied cormorant, *Phalacrocorax varius*, and the Black-faced shag, *Leucocarbo fuscescens*.

The first four pairs of postacetabular foramina are about twice as long as wide in *Phalacrocorax* and relatively broader and less than twice as long as wide in *Microcarbo*. The concave preacetabular lateral edge of ilium is relatively long in *Microcarbo* and short in *Phalacrocorax*. The pelvis is relatively longer and more slender in *Phalacrocorax* than in *Microcarbo*.

Because WAM 70.2.10 fits the above characters of *Microcarbo*, except for the femora, I propose a new specific name for it.

Microcarbo serventyorum sp. nov.

Etymology

In honour of the Serventy brothers, Dom and Vincent, for their contributions to our knowledge



FIGURE 2. Dorsal view of pelvis. *Microcarbo serventyorum* WAM 70.2.10.

of the Australian cormorants and shags (Serventy 1938, 1939, Serventy & White 1943, Serventy *et al.* 1971).

Diagnosis

A cormorant slightly smaller than species of *Microcarbo* and *Phalacrocorax*, relatively long preacetabular concave lateral edge on ilium; relatively broader first four pairs of postacetabular foramina adjacent to narrower ilia, and much larger 8th pair than in species of *Microcarbo* and *Phalacrocorax*. Parapophyses between 7th and 8th pair extend cranio-laterally and not laterally as in *Microcarbo* and *Phalacrocorax* (See figs 1–4).

Measurements of WAM 70.2.10 are generally more than ± 3 sd away from mean measurements of the smallest extant species of *Phalacrocorax*, and differ from all extant species of *Microcarbo*. These differences are most marked in the length of the dorsal ridge of the pelvis, the length of the 8th postacetabular foramen, and the proximal width of the femur (Table 1).



FIGURE 3. Caudal view of left femur. Left: *Microcarbo* ANWC BS-1419. Right: *Phalacrocorax sulcirostris* ANWC BS-1310.

Holotype

WAM 70.2.10, a pelvis with associated femora and caudal vertebrae.

DISCUSSION

Australasia has four sympatric species of cormorants that occur on inland waters, which is

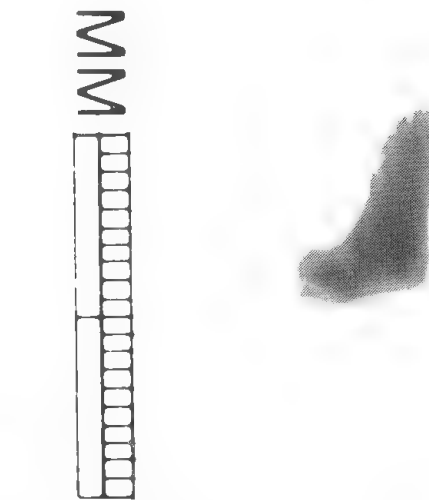


FIGURE 4. Caudal view of left femur. *Microcarbo serventyorum* WAM 70.2.10.

more than anywhere in the world. Two are large, the Great cormorant, *Phalacrocorax carbo*, and the Pied cormorant, *P. varius*, and forage in rivers and large lakes and lagoons. Two are small, the Little black cormorant, *P. sulcirostris*, and the Little pied cormorant, *Microcarbo melanoleucos*. *Phalacrocorax sulcirostris* forages mainly in flocks in open water and *M. melanoleucos* forages in ponds, streams and along edges of large water bodies. Species of *Phalacrocorax* swim rapidly with their feet behind the body, while species of *Microcarbo* swim slowly with their feet beside

TABLE 1. Measurements (mm) of pelvis and femora of species of *Microcarbo* and *Phalacrocorax*.

A: \bar{x} (sd, range, n)

	<i>M. melanoleucos</i>	<i>P. sulcirostris</i>	<i>P. olivaceus</i>
TL	82 (4, 73–88, 13)	97 (6, 84–113, 25)	102 (7, 95–109, 3)
WA	25 (1.4, 23–28, 15)	27 (1.4, 24–30, 25)	30 (2.3, 27–31, 3)
LF	2.8 (0.4, 2.0–3.3, 14)	3.2 (0.3, 2.6–3.9, 25)	3.3 (0.4, 2.9–3.6, 3)
PW	11 (0.7, 9–12, 14)	12 (0.8, 11–14, 25)	13 (1.2, 12–14, 3)
DH	5.0 (0.3, 4.5–5.5, 14)	4.9 (0.3, 4.3–5.3, 25)	5.6 (0.6, 4.9–6.0, 3)
TL/WA	3.2 (0.13, 3.0–3.5, 13)	3.6 (0.18, 3.2–38, 25)	3.4 (0.17, 3.2–35, 3)

B: n = 1

	<i>M. africanus</i>	<i>M. coronatus</i>	<i>M. pygmaeus</i>	<i>M. niger</i>	<i>M. serventyorum</i>
TL	79	77	81	77	71
WA	25	26	26	23	22
LF	2.5	2.7	2.7	2.9	5.1
PW	11	11	11	9	7.5
DH	4.7	4.6	5.0	4.1	4.3
TL/WA	3.2	3.0	3.1	3.3	3.2

Abbreviations: TL = length of medium dorsal ridge of pelvis, WA = width between tips of antitrochanters, LF = length of 8th postacetabular foramen, PW = proximal width of femur, and DH = depth of head of femur.

the body. Exaggeration of pelvic features that distinguish extant species of *Microcarbo* from those *Phalacrocorax* suggest that *Microcarbo serventyorum* was even more adept at foraging in confined bodies of water. Its small size and discovery in a peat swamp suggest that *M. serventyorum* lived in marshes with dense vegetation, small pools and narrow creeks. It may have had a niche distinct from that of the other four species of cormorant and may have been part

of the Australasian divergence I postulated (van Tets 1976).

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BIRDS FROM THE BLUFF DOWNS LOCAL FAUNA, ALLINGHAM FORMATION, QUEENSLAND

WALTER E. BOLES & BRIAN MACKNESS

Summary

A small number of bird fossils have previously been recorded from the early Pliocene freshwater, fluviate and lacustrine deposits of the Allingham Formation, northwest of Charters Towers, northeastern Queensland. There has been significant avifaunal discoveries made during recent excavations of the site, most of these being waterbirds. The number of taxa now recognised has almost trebled from previous published accounts and includes at least seven orders, ten families and 15 species-level taxa. A new subspecies of the Purple swamphen, *Porphyrio porphyrio nujagura* subsp. nov., is described. The earliest occurrences of the genera *Anhinga*, *Ardea*, *Cereopsis* and *Proregulus* in the Australian avifaunal fossil record are also reported. The potential role that the study of fossil birds can play in palaeocological reconstruction is discussed.

BIRDS FROM THE BLUFF DOWNS LOCAL FAUNA, ALLINGHAM FORMATION, QUEENSLAND.

WALTER E. BOLES & BRIAN MACKNESS

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A small number of bird fossils have previously been recorded from the early Pliocene freshwater, fluvial and lacustrine deposits of the Allingham Formation, northwest of Charters Towers, northeastern Queensland. There has been several significant avifaunal discoveries made during recent excavations of the site, most of these being waterbirds. The number of taxa now recognised has almost trebled from previous published accounts and includes at least seven orders, ten families and 15 species-level taxa. A new subspecies of the Purple swamphen, *Porphyrio porphyrio nujagura* subsp. nov., is described. The earliest occurrences of the genera *Anhinga*, *Ardea*, *Cereopsis* and *Procygna* in the Australian avifaunal fossil record are also reported. The potential role that the study of fossil birds can play in palaeoecological reconstructions is discussed.

Walter E. Boles, Division of Vertebrate Zoology, Australian Museum, 6–8 College Street, Sydney. Brian Mackness, School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington New South Wales 2033. Manuscript received 31 July 1993.

Birds have long been considered to be of secondary importance in the examination of fossil assemblages, with the paucity of their occurrence in the fossil record being cited as just one of the reasons for this cursory treatment (Olson 1985). The Australian fossil avifaunal record stretches back to the Cretaceous (Vickers-Rich 1991) and, although there has been a considerable increase in the investigation of fossil birds in recent years, most Tertiary studies have been taxonomic in nature, usually focussing on a single group (e.g. Miller 1963, 1966; Rich 1979; van Tets 1974). The interpretation of palaeoenvironments using fauna has relied almost exclusively on mammals, and indeed the 'Local Fauna' concept (Tedford, 1970) has this as its foundation.

In recent years, however, with an increasing number of palaeornithologists working in Australia, birds are being used more and more both as biostratigraphic markers (Rich 1979) and as palaeoecological indicators (Boles 1993; Baird 1993).

A variety of taxa has been recovered from the early Pliocene freshwater fluvial and lacustrine deposits of the Allingham Formation, northwest of Charters Towers, northeastern Queensland (Archer 1976, Bartholomai 1978, Archer & Dawson 1982, Archer 1982, Rich & van Tets 1982). Collectively this assemblage has been called the Bluff Downs Local Fauna (Archer 1976). The only bird mentioned in the original

description of the fauna was *Xenorhynchus* [= *Ephippiorhynchus*] *asiaticus* (Archer 1976). Subsequently Rich & van Tets (1982) cited five taxa: *Xenorhynchus* cf. *X. asiaticus*, *Threskiornis* sp., cf. *Dendrocygna* sp., *Numenius* sp. and Charadriiformes. Rich *et al.* (1991) also listed five taxa: *Xenorhynchus* [= *Ephippiorhynchus*] *asiaticus*, *Threskiornis* sp., *Cygnus* sp., *Dendrocygna* sp. and *Numenius* sp. None of these listings offered further elaboration.

MATERIALS AND METHODS

Measurements were taken with vernier calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm. Terminology of bones is primarily from Baumel (1979). Where comparisons were made with published measurements, the methods of measuring followed those adopted in the comparative study; otherwise these largely followed those illustrated by Steadman (1980). Specimens are currently held at the Queensland Museum. All the fossil material examined and all modern specimens used for comparisons were considered to be adults, based on the absence of a '... pitted surface of the bone and incomplete ossification of the articular facets' (Campbell 1979: 17).



SYSTEMATICS

PHALACROCORACIDAE

Phalacrocorax sulcirostris

(Fig. 1a,b)

Material

Proximal right humerus (QM F23242), distal right humerus (QM F23241), possibly from the same bone. Measurements: proximal width 16.8 mm, distal width 11.7 mm, depth of *condylus dorsalis* 7.9 mm. Locality: EVS Site.

Characters

The two fragments are considered to belong to the same species, and possibly the same individual, on the basis of size and configuration. The proximal end is referred to the Phalacrocoracidae on the basis of the reduced *crista pectoralis*, very broad *impressio m. coracorbrachialis* and broad, deep *sulcus ligamentosus transversus*. The distal fragment has a deeply excised *fossa m. brachialis*, which among extant Australian species occurs in *P. sulcirostris* and *P. varius* (Siegel-Causey 1988). The fossil agrees in size with *P. sulcirostris* (proximal width 16.2–17.2 mm, distal width 11.4–13.1 mm, depth of *condylus dorsalis* 7.9–8.6 mm), and is smaller than *P. varius* (proximal width 19.1–21.8 mm, distal width 13.1–14.1 mm, depth of *condylus dorsalis* 9.1–9.8 mm).

Remarks

The Little Black Cormorant is widespread in wetlands, preferring open water greater than one metre deep, including large lakes, areas with flooded or fringing trees, and swamps with permanent or semi-permanent water (Marchant & Higgins 1990).

ANHINGIDAE

Anhinga sp.*Material*

Proximal right humerus (QM F23653); right carpometacarpus (QM F25776). This material represents a new species and is being described (B. M.) elsewhere. Locality: QM F23653, EVS Site; QM F25776, Main Site.

Remarks

Darters prefer smooth, open water at least 0.5 m deep, including permanent waterbodies, large lakes with shallow vegetated edges and semi-permanent swamps (Marchant & Higgins 1990).

ARDEIDAE

cf. *Ardea picata*

(Fig. 1e)

Material

Distal right tibiotarsus (QM F23243). Measurements: distal width 7.7 mm, depth of *condylus lateralis* 7.4 mm, depth of *condylus medialis* 7.9 mm. Locality: EVS Site.

Characters

The fossil is smaller and relatively more gracile than *Egretta novaehollandiae*, *E. garzetta*, *A. intermedia*, *Ixobrychus flavicollis* and *Nycticorax caledonicus*, but a good match in size and robustness for *Ardea picata* (distal width 6.3–8.0 mm, depth of *condylus lateralis* 6.5–7.6 mm, depth of *condylus medialis* 6.6–7.9 mm). It is not possible to assign the distal tibiotarsus to any particular genus of herons on morphological features. Payne & Risley (1976) found no consistent differences in the tibiotarsi within this family.

◀ FIGURE 1. Avian fossils from the Bluff Downs Local Fauna. Bars equal 10 mm. Bars are shared by A and B, and by M, N and O. Queensland Museum registration numbers are given in parentheses.

A. *Phalacrocorax sulcirostris*, proximal right humerus (F 23242); B. *Phalacrocorax sulcirostris*, distal right humerus (F 23241); C. *Threskiornis* sp. cf. *T. molucca*, cranial right coracoid (F 23257); D. *Threskiornis* sp. cf. *T. molucca*, distal right tarsometatarsus (F 23256); E. *Ardea* sp. cf. *A. picata*, distal right tibiotarsus (F 23243); F. *Ephippiorhynchus asiaticus*, proximal left humerus (F 23244); G. *Ephippiorhynchus asiaticus*, distal left humerus (F 23245); H. *Phoenicopterus* sp. cf. *P. ruber*, distal right tarsometatarsus (F 23252); I. *Dendrocygna arcuata*, proximal right humerus (F 23248); J. *Progora* sp. cf. *P. naracoortensis*, carpometacarpus (F 23258); K. *Progora* sp. cf. *P. naracoortensis*, proximal left tarsometatarsus (F 23259); L. *Porphyrio porphyrio nujagura* subsp. nov., proximal right tarsometatarsus (F 23250); M. Rallidae gen. and sp. indet. 2, distal left tarsometatarsus (F 23255); N. Rallidae gen. and sp. indet. 1, distal left tibiotarsus (F 23254); O. *Porzana* sp., distal left tarsometatarsus (F 23253); P. cf. *Numenius* sp., distal right femur (F 23251).

Remarks

Virtually all herons are associated with water, the type of wetland preferred and the manner in which it is utilised depending on the species. The Pied Heron occurs in shallow wetlands, including floodplains and swamps (Marchant & Higgins 1990).

CICONIIDAE*Ephippiorhynchus asiaticus*

(Fig. 1f,g)

Material

Proximal left humerus (QM F23244); distal left humerus (QM F23245). Measurements: proximal width 44.8 mm, distal width 34.4 mm, depth of *condylus dorsalis* 18.7 mm. A '... fragment of tarsometatarsus (QM F7036)' cited by Archer (1976: 385) was not examined. Locality: QM F23244 AB Site; QM F7036, QM F23245 Main Site.

Characters

The proximal fragment agrees with the Ciconiidae and differs from the Gruidae, the only other similar taxon, by having *caput humeri* proportionally shorter, *intumescencia* less inflated and *fossa pneumaticipitalis* larger. The distal fragment resembles the former family, but not the latter, by having *tuberculum supracondylare ventrale* narrow and ridge-like, and *processus supracondylaris dorsalis* prominently produced.

Remarks

The Black-Necked Stork, Australia's only extant member of this family, inhabits mainly open water up to 0.5 m deep, including extensive sheets over grassland, shallow swamps and pools on floodplains (Marchant & Higgins 1990).

THRESKIORNITHIDAE*Threskiornis* sp. cf. *T. molucca*

(Fig. 1 c,d)

Material

Cranial right coracoid (QM F23257); distal right tarsometatarsus missing *trochlea metatarsi IV* (QM F23256). Measurements: coracoid, cranial end of *processus acrocoracoideus* to caudal end of *cotyla scapularis* 20.6 mm, depth of *processus acrocoracoideus* 9.4 mm; tarsometatarsus, depth of *trochlea metatarsi III*

c. 8.0 mm, dorsal length of *trochlea metatarsi III* 8.2 mm. Locality: QM F23256 EVS Site; QM F23257 Main Site.

Characters

The tarsometatarsus is assigned to *Threskiornis* rather than *Platalea* because *trochlea metatarsi II* agrees with the former in being less recessed plantarly relative to *trochlea metatarsi III* (in medial view). It agrees in size with *molucca* (depth of *trochlea metatarsi III* 8.4 mm, plantar length of *trochlea metatarsi III* 8.0 mm), which is larger than *spiniacollis* (depth of *trochlea metatarsi III* 7.3–7.4 mm, plantar length of *trochlea metatarsi III* 7.1–7.3 mm).

Allocation of the coracoid to *Threskiornis* rather than *Platalea* is on the basis of having a narrower *processus acrocoracoideus* (in dorsal view), *cotyla scapularis* proportionally further from *processus acrocoracoideus*, and *processus procoracoideus* curving less mediad.

Living *T. spiniacollis* and *T. molucca* are not separable on measurements that can be taken on the fossil coracoid (cranial end of *processus acrocoracoideus* to *cotyla scapularis*: *spiniacollis* 20.4–21.8 mm, *molucca* 20.2–22.8 mm; depth of *processus acrocoracoideus*: *spiniacollis* 11.7–12.1 mm, *molucca* 11.3–12.1 mm). These species differ somewhat in robustness of the shaft; however, damage to the Bluff Downs material precludes comparison. The coracoid is referred to the same taxon as the tarsometatarsus. Because material is limited and the living species are morphologically quite similar, a more definite identification is not made.

Remarks

The Australian White Ibis habitat preferences include shallow water over soft substrates, in swamps and open water, and muddy flats (Marchant & Higgins 1990).

PHOENICOPTERIDAE*Phoenicopterus* sp. cf. *P. ruber*

(Fig. 1h)

Material

Partial distal right tarsometatarsus lacking *trochlea metatarsi IV* (QM F23252). Measurements: medial depth of *trochlea metatarsi II* c. 7.9 mm, lateral depth of *trochlea metatarsi II* 8.4 mm, dorsal width of *trochlea metatarsi III* 10.3 mm, lateral depth of *trochlea*

metatarsi III c. 9.1 mm, dorsal width of *trochlea metatarsi III* c. 7.6 mm, plantar length of *trochlea metatarsi III* 11.7 mm. Locality: Main Site.

Characters

This specimen is identified as a flamingo on the basis of the following characters (most from Rich *et al.* 1987): *trochlea metatarsi II* short relative to *trochlea metatarsi III*; distal end of *trochlea metatarsi II* broader than plantar border; *trochlea metatarsi II* twisted plantarly and laterally from front of tarsometatarsus; and *trochlea metatarsi III* narrow and deep. Reference of this fragment to this species is made on the basis of size rather than on diagnostic morphology.

The measurements of the Bluff Downs specimen are a good match for those of extant *P. ruber* given by Rich *et al.* (1987), and the specimen is therefore tentatively assigned to this taxon. This follows the practice of Rich *et al.* (1987: 207), who, faced with limited and undiagnostic material, segregated the forms on size and '... provisionally retained the generic and specific names that have priority as a convenience until more complete material allows a better evaluation of the systematic positions of the Pliocene and Quaternary flamingoes of Australia'.

Remarks

There are few records of flamingoes in Australia away from the centre of the continent. Rich *et al.* 1991 have recorded an undetermined flamingo from the late Miocene Alcoota Local Fauna, northern Australia. Living *P. ruber* of Africa frequents mainly saline or alkaline lakes, estuaries and lagoons, seldom alighting on fresh water (Brown *et al.* 1982). Similar conditions have been proposed for central Australian lake deposits yielding flamingo remains. The Alcoota Locality during the late Miocene is considered by Murray & Megirian (1992: 214) to have represented '... a small but permanent, possibly spring-fed pond or lake, sometimes expanding to a temporary, large, shallow lake.'

ANATIDAE

Cygnus atratus

Remarks

This taxon was cited by Vickers-Rich (1991) without further elaboration. This material has not been examined in this study. Locality: Main Site.

Cereopsis sp.

Material

A proximal carpometacarpus fragment (QM F23260). This material, probably representing the extant species *C. novaehollandiae*, will be described (B.M.) elsewhere. Locality: EVS Site.

Remarks

This species inhabits grasslands and terrestrial wetlands, occasionally entering water.

Dendrocygna arcuata

(Fig. 1i)

Material

Proximal right humerus (QM F23248). Measurements: proximal width c.18.3 mm, depth of *caput humeri* 6.0 mm. Locality: Main Site.

Characters

The Anserinae and Dendrocygninae are separated from other Anatidae by the combination of prominent capital shaft ridge directed towards the *caput humeri*, attachment for *caput ventrale* of *M. humerotriceps* extending virtually to *caput humeri*, and area of attachment of *M. pectoralis* on the *tuberculum dorsale* is elevated and somewhat circular (Woolfenden 1961). The Anserinae is unrepresented in Australasia except by the aberrant *Cereopsis*, which is diagnosable by several unique characters. The Bluff Downs specimen is an excellent fit for *Dendrocygna*, agreeing in size with *D. arcuata*, the smaller of the two Australian species.

Remarks

The Water Whistling-Duck prefers fresh, deep permanent waters with emergent vegetation (Marchant & Higgins 1990).

Nettapus sp.

Material

An almost complete left carpometacarpus (QM F23249). This material probably represents a new species and will be described (B.M.) elsewhere. Locality: EVS Site.

Remarks

Pygmy-geese are wholly aquatic on terrestrial wetlands, preferably deep (greater than 1m), permanent water bodies, with abundant floating

and submerged vegetation (Marchant & Higgins 1990).

MEGAPODIIDAE

Progura sp. cf. *P. naracoortensis* (Fig. 1j,k)

Material

Carpometacarpus (QM F23258) lacking *os metacarpale minor*. Proximal left tarsometatarsus (QM F23259) lacking most of the *hypotarsus*. Measurements: carpometacarpus, proximal width (dorsal) 17.5 mm, (ventral) 15.0 mm; tarsometatarsus, proximal width 19.5 mm. Locality: EVS Site.

Characters

A tentative identification has been made on size. Van Tets (1974) published measurements for the two known species: proximal width of tarsometatarsus, *P. naracoortensis* 21–23 mm, *P. gallinacea* 26–29 mm; dorsal and ventral widths of carpometacarpus, *P. gallinacea* 27 x 16 mm; a carpometacarpus of *P. naracoortensis* was not available. The Bluff Downs material is smaller and older than that of either species. Here it is tentatively referred to the smaller *P. naracoortensis*, but it may represent an undescribed species.

The tarsometatarsus of *Progura* is separated from that of extant genera of Australian megapodes by the following combination of characters: hypotarsus situated more laterad, *sulcus hypotarsi* more laterally situated relative to *eminentia intercondylaris*, *cotyla medialis* nearly size of *cotyla lateralis* in cranial view with dorsal border rounded and projecting dorsally about the same extent as *cotyla lateralis*, medial border of *corpus tarsometatarsi* straight (less concave), and *sulcus extensorius* broader and deeper and extending further distad.

The carpometacarpus is distinguished by its combination of *processus extensorius* more proximally directed, proximal border of *facies articularis radiocarpalis* of *trochlea carpalis* rounded (not pointed), caudal border of *facies articularis ulnocarpalis* of *trochlea carpalis* rounded (not flattened) and extended ventrally only slightly more than *facies articularis radiocarpalis*, and *os metacarpale majus* slightly caudally curved.

Remarks

Previous records of *Progura* are from coastal

and subcoastal areas of eastern and southeastern Australia. Not enough is known about the ecology of these animals for them to be useful bioecological indicators. Van Tets (1974) hypothesised that, based on relative leg lengths, the longer-legged *P. gallinacea* was a rainforest species, whereas *P. naracoortensis* inhabited open scrub land. Van Tets (1984) later suggested that, because these two species are usually found together, they could represent a single, sexually dimorphic species.

RALLIDAE

Porzana sp. (Fig. 1o)

Material

Distal left tarsometatarsus (QM F23253). Measurements: distal width 4.3 mm. Locality: EVS Site.

Characters

This specimen is larger than *Porzana tabuensis* (distal width 3.7 mm) or *P. pusilla* (3.3 mm) and about the same size as *P. fluminea* (4.3 mm) and *P. cinereus* (4.7 mm). Compared with these latter two species, *trochlea metatarsi* are thinner and more splayed, *trochlea metatarsi II* appears slightly less directed plantarad, and *incisurae intertrochlearis* are wider. The specimen is abraded on the trochlear surfaces, and some of these differences could be artefacts of this wear. Osteological characters given by Olson (1970) and Steadman (1986) between *P. cinerea* and other species of *Porzana* are not relevant to this partial element.

Remarks

Most rails are associated with water. The smaller species, including most *Porzana*, are usually shy, spending most of their time in dense waterside vegetation. *Porzana cinerea* also requires floating vegetation.

Genus and species indet. 1 (Fig. 1n)

Material

Distal left tibiotarsus (QM F23254). Distal width 5.1 mm, depth of *condylus lateralis* c. 5.3 mm, depth of *condylus medialis* c. 5.3 mm. Locality: EVS Site.

Remarks

The fossil represents a small to medium rail between the sizes of *Porzana cinereus* (distal width 4.2 mm, depth of *condylus lateralis* 3.9 mm, depth of *condylus medialis* 4.1 mm) and *Gallirallus philippensis* (distal width 6.0 mm, depth of *condylus lateralis* 6.0 mm, depth of *condylus medialis* 6.0 mm). There are several extant Australasian genera within this size range with which the specimen should be compared, *Dryolimnas* (*sensu* Olson 1973), *Rallina* and *Rallacula*.

Genus and species indet. 2.

(Fig. 1m)

Material

Distal left tarsometatarsus (QM F23255). Measurements: distal width 7.1 mm, depth of *trochlea metatarsi III* 3.8 mm. Locality: EVS Site.

Characters

This specimen comes from a larger and somewhat more robust species than the previous indeterminate rail. It is similar in size to *Amaurornis olivacea* (distal width 6.7–6.9 mm, depth of *trochlea metatarsi III* 3.2–3.6 mm) and *Gallinula ventralis* (distal width 7.4 mm, depth of *trochlea metatarsi III* 4.3 mm). This fossil is also similar in morphology to *A. olivacea*, and probably could be tentatively referred to that species; however, it seems prudent to await more extensive material and comparisons with a greater range of genera before taking this action.

Porphyrio porphyrio nujagura subsp. nov.

(Fig. 1l)

Material

Proximal right tarsometatarsus (QM F23250). Measurements: proximal width 9.7 mm, proximal depth 11.4 mm, length of *hypotarsus* 10.4 mm, width of *hypotarsus* 5.6 mm. Locality: EVS Site.

Characters

Agrees with *Porphyrio* and differs from other genera of Australian rails, including the genera of larger forms (*Gallinula*, including *Tribonyx*; *Fulica*; *Gallirallus australis*) by having a distally directed projection on the plantodistal end of the *hypotarsus* (in other genera, the *hypotarsus* curves smoothly into the shaft).

There are four Recent species of *Porphyrio* from Australasia: three flightless Australasian species (*mantelli*, New Zealand; *albus*, Lord Howe Island – extinct; and *kukwiedei*, New Caledonia – extinct; Balouet & Olson 1989); and *porphyrio*, the only member of the genus now occurring in Australia. The first three are much larger and robust than *porphyrio*. The Bluff Downs specimen shows no morphological differences from *porphyrio* but is smaller than either sex of this sexually size dimorphic species (Australian *porphyrio*: proximal width 10.7–12.5 mm, proximal depth 12.4–13.7 mm, length of *hypotarsus* 11.0–13.0 mm, width of *hypotarsus* 6.2–6.9 mm). Compared with measurements given by Steadman (1988: Table 2), it is also smaller than most extralimital populations of the *P. porphyrio* superspecies, except *P. porphyrio* from Bechuanaland and *P. poliocephalus* of Thailand.

Etymology

The specific name is from the Gugu-Yalanji dialect word *nujagura*, meaning 'prehistoric times' (Oates *et al.* 1964).

Remarks

The only extant Australian species of comparable size not examined was *Eulabeornis castaneoventris*, a mangrove specialist, for which no skeletons exist. The end of the shaft is jagged, indicating that the break occurred before fossilisation. This individual was probably a victim of a predator or scavenger. The Purple swamphen prefers permanent freshwaters with good cover of rushes and other larger waterplants, at least along the water's edge, usually in the proximity of more open grazing areas (Marchant & Higgins 1993).

SCOLOPACIDAE

cf. *Numenius* sp.

(Fig. 1p)

Material

Distal right femur (QM F23251). Measurements: distal width 10.0 mm, depth of *condylus lateralis* 8.7 mm, depth of *condylus medialis* c. 7.0. Locality: Main Site.

Characters

This specimen appears to represent a large sandpiper. It is substantially larger than all Australasian taxa except for *Numenius*, for which it is also a good match in morphology. Because

the distal femur has limited diagnostic value and the bone is slightly abraded, identification is not attempted beyond cf. *Numenius* sp.

Remarks

Some members of this family are restricted to coastal areas; others occur in freshwater wetlands (Lane 1987). Larger *Numenius* species are coastal, whereas *N. minutus* extends well into subcoastal regions.

DISCUSSION

Taphonomy

All fossils were recovered from a series of massive lacustrine clays from Main Quarry (Archer 1976) and Elaine's Vertebrae Site (Mackness unpublished information). Most of the bones were not complete and showed post-depositional breakage and fragmentation. An exception was the tarsometatarsus of *Porphyrio porphyrio nujagura*, the jagged edge of which suggested predation or scavenging while the body was still relatively fresh. There was little evidence of transportation wear and, even though there was no articulation, it is probable that the birds died in reasonable proximity to the site of deposition. An examination of bone textures suggests that there was little subaerial prediagenetic exposure and that most bones were quickly buried or submerged.

Vickers-Rich (1991) suggested a bias in avifaunal fossil deposits toward medium-sized birds (e.g. ducks, flamingos, burhinids) and larger birds (emus) to the exclusion of smaller birds. Although the bird assemblage recovered to date is consistent with this prediction, large scale wet-screening of sediments presently being undertaken may result in the recovery of smaller birds. The depositional environment obviously favours the preservation of waterbirds: these are also common

in central Australian Tertiary sites (Vickers-Rich 1991). The proportions of the different bone elements found fossilised at Bluff Downs are summarised in Figure 2. All are regarded to be the most durable elements (Napawongse 1981; Rich & Baird 1986; Vickers-Rich 1991).

Palaeoecology

Archer (1976) has suggested that the Bluff Downs Local Fauna may have been riparian. The large number of non-avian fossils recovered from the Bluff Downs site include both terrestrial and aquatic forms, with neither predominating. The mammals provide no definitive indication of what the terrestrial environment may have been like, although a typically rainforest-dwelling pseudocheirid possum is presently being described (B.M.), along with an enigmatic family of marsupials (Mackness *et al.* 1993).

Three types of crocodiles have been recovered, including two large aquatic and one terrestrial form (Willis & Mackness in prep.). Studies of the molluscan fauna have revealed a diverse suite of species, some requiring specific aquatic niches that range from high energy fluvial environments to stagnant lacustrine regimes (Mackness, unpublished data). It is evident from this faunistic 'mix' that there was a complex series of aquatic environments available either ephemerally or on a permanent basis.

Various authors (Frith 1959, Braithwaite & Frith 1969, Braithwaite 1975, Fjelds  1985) have suggested a relationship between the distribution of waterbird species and habitat types. Fjelds  (1985) found poor correlation between avian communities and classifications based on vegetation types. Indicator species, e.g. *Porphyrio* and *Phalacrocorax*, are present in several of Fjelds 's classifications. Given the taphonomic evidence of minimal transportation and the nature of the sediments themselves, the Bluff Downs avifauna appears to be a biocoenotic assemblage, which may represent several depositional episodes. While most of the taxa identified, or their closest extant relatives, are relatively nonspecific in their preferences for wetland types, some utilise a range of microhabitats within wetland environments. Living species of *Nettapus* are more strict in their requirements than most, being generally confined to deeper water with considerable floating vegetation.

Living *Cereopsis novaehollandiae* graze on grasslands, whereas living phoenicopterids are

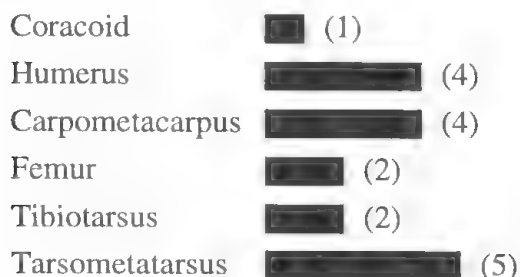


FIGURE 2. Summary of avian skeletal elements recovered from Bluff Downs Site.

TABLE 1. Comparison of Australian Pliocene avifaunal assemblages. Data for Chinchilla and Kanunka from Rich *et al.* (1991) and Vickers-Rich (1991).

Family	Bluff Downs	Chinchilla	Kanunka
Casuariidae	—	X	X
Pelecanidae	—	X	X
Phalacrocoracidae	X	X	X
Anhingidae	X	X	X
Ardeidae	X	—	X
Ciconiidae	X	—	X
Threskiornithidae	X	—	—
Phoenicopteridae	X	—	X
Anatidae	X	X	X
Accipitridae	—	—	X
Gruidae	—	—	X
Megapodidae	X	X	—
Rallidae	X	X	—
Otididae	—	—	X
Scolopacidae	X	—	—
'Charadriiformes'	—	X	X

normally found in saline environments today. Disregarding these novelties, the remaining taxa comprise a waterbird community that differs little from that which now occurs in tropical Australia, such as in the wetlands of Kakadu National Park, Northern Territory, an area supporting seasonal floodplains, waterholes, rivers, ephemeral swamps and permanent lakes. From the avian assemblage, it is probable that at least part of Bluff Downs consisted of similar wetlands during the Pliocene.

Comparisons with other Pliocene faunas

Most Pliocene deposits have yielded bird fossils. Many are too fragmentary for identification while others have not yet been studied (Vickers-Rich 1991). Apart from the Bluff Downs Local Fauna, both the Chinchilla and Kanunka Local Faunas have significant avian components (Table 1). All three avifaunas are considered to be wetland assemblages, with the dominant families represented containing mostly wetland specialists. In these, most of the same families are represented. However long-legged wading birds

(Ciconiiformes, Phoenicopteriformes) are absent from Chinchilla.

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MIMICRY IN ANKYLOSAURID DINOSAURS

TONY THOLBORN

Summary

The tail club of Late Cretaceous ankylosaurid dinosaurs is usually regarded as a weapon to deter predators. However, the effective reach of the club was clearly constrained by the shortness and limited flexibility of the tail as a whole. Analogies with the defensive adaptations of butterflies and other insects indicate that the ankylosaurid tail club may represent a 'dummy head' that diverted predators from the true head. Simulated escape movements of that false head could have elicited the attack response of persistent aggressors, thus bringing them within striking range; thereupon the tail club would have performed its third function, as a weapon, to greatest effect. In performing such deceptive functions, the ankylosaurid tail club would qualify as an example of mimicry, seemingly the first to be identified among dinosaurs.

MIMICRY IN ANKYLOSAURID DINOSAURS

TONY THULBORN

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The tail club of Late Cretaceous ankylosaurid dinosaurs is usually regarded as a weapon to deter predators. However, the effective reach of the club was clearly constrained by the shortness and limited flexibility of the tail as a whole. Analogies with the defensive adaptations of butterflies and other insects indicate that the ankylosaurid tail club may represent a 'dummy head' that diverted predators from the true head. Simulated escape movements of that false head could have elicited the attack response of persistent aggressors, thus bringing them within striking range; thereupon the tail club would have performed its third function, as a weapon, to greatest effect. In performing such deceptive functions, the ankylosaurid tail club would qualify as an example of mimicry, seemingly the first to be identified among dinosaurs.

Tony Thulborn, Vertebrate Palaeontology Laboratory, Department of Zoology, University of Queensland, Brisbane, Queensland 4072. Manuscript received 21 April 1993.

Ornithischians of the suborder Ankylosauria are often epitomized as 'armoured dinosaurs' or 'reptilian tanks' on account of their exuberant developments of dermal bone (e.g. Charig 1979; Norman 1985; Carroll 1988; Coombs & Maryanska 1990). Among these dinosaurs the skull was protected by a helmet-like covering of osteoderms, while the neck, back, flanks and tail were shielded by a remarkable array of bony studs and plates, often elaborated into keels or spikes (Fig. 1). In addition, the members of one ankylosaur group, the family Ankylosauridae, carried a conspicuous deterrent weapon in the form of a bony club at the tip of the tail (Fig. 2). It is often supposed that ankylosaurids would sweep this weapon sideways to strike at the feet and legs of their aggressors (e.g. Charig 1979; Coombs 1979; Norman 1985).

Conventional thinking on the defensive capabilities of the armoured dinosaurs has been well summarized by Coombs & Maryanska (1990: 482–3):

'When attacked by predators, ankylosaurs primarily defended themselves passively, relying on their extensive armor and low-slung, difficult-to-overturn body conformation. Outrunning of predators seems unlikely. Ankylosaurids may have used their tail clubs for active defense by sweeping it just above the ground to strike at the fragile ankles of an attacking predator...'

This paper examines more closely the defensive capabilities of the ankylosaurid dinosaurs, giving particular attention to the role of the tail club.

THE ANKYLOSAURID TAIL CLUB

The deterrent value of a tail club depends on its effective reach and, hence, on the length and flexibility of the entire tail. Surprisingly, the ankylosaurid tail was rather short and somewhat inflexible (Fig. 2). For instance, the ankylosaurid *Euoplocephalus tutus* possessed only 20 caudal vertebrae (excluding the first, which was joined to the sacrum, and an unknown number built into the terminal club); by comparison, the clubless tail of the nodosaurid *Sauropelta edwardsi* (family Nodosauridae) comprised 40 to 50 vertebrae (Carpenter 1982, 1984). Long transverse processes probably imposed some constraint on flexures at the base of the tail, and the distal caudal vertebrae were deeply internested, sheathed in ossified tendons and amalgamated into a rigid 'handle' to the tail club (Coombs & Maryanska 1990; Carpenter 1982). Consequently, the tail was flexible only in its proximal half, and then to a limited degree. It is inconceivable that the tail club could have been swung alongside the animal's flank, or across its back, or anywhere near the head, neck and shoulders.

It is sometimes implied that special defensive behaviour might have compensated for the limited reach of the tail club. For example, Norman supposed (1985: 168) that the ankylosaurid *Euoplocephalus* was sufficiently agile to avoid the lunges of a tyrannosaur while manoeuvring into position to retaliate. However, the exceptionally broad body of ankylosaurs probably conferred great stability (Carpenter 1984; Norman 1985;

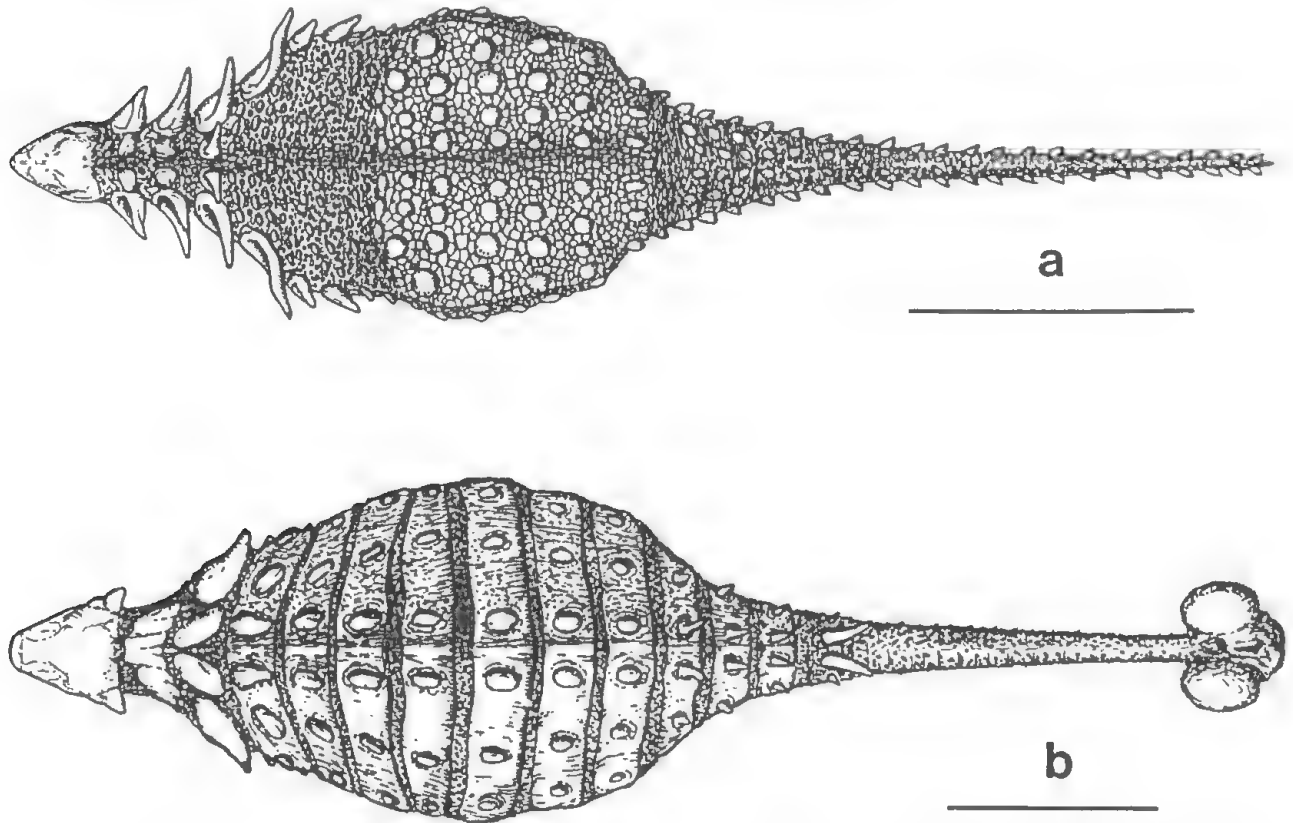


FIGURE 1. General body form of ankylosaurian dinosaurs. **a**, Restoration of the nodosaurid ankylosaur *Sauropelta edwardsi* in dorsal view (adapted from Carpenter 1984). **b**, Comparative restoration of the ankylosaurid ankylosaur *Euoplocephalus tutus* (adapted from Carpenter 1982). Each scale bar indicates 1 metre.

Bakker 1986; Coombs & Maryanska 1990), so that these animals were not easily overturned by predators. Such inherent stability is the antithesis of agility – which, in essence, is controlled instability. It is difficult to imagine that a single ankylosaurid, however agile, could turn rapidly enough to fend off two or more predators hunting in cooperation.

Overall, it seems as if the ankylosaurid tail club could have functioned as an effective weapon only if an aggressor strayed within the rather limited reach of the tail.

BEHAVIOUR OF PREDATORY DINOSAURS

Big theropod dinosaurs, or ‘carnosaurs’ *sensu lato*, were probably the only predators capable of killing and dismembering the heavily-armoured ankylosaurids, which grew to a length of 6 metres and a weight of several tonnes. Presumably, carnosaurs attacked the most vulnerable regions of their prey, namely the head and neck. This strategy has several advantages (Ewer 1968): an attack to the head may confuse and disorient the prey, thereby reducing the risk of retaliation; there is

great likelihood of inflicting fatal injuries—by severing or puncturing the spinal cord, the trachea or major blood vessels; and, finally, a rapid kill reduces the risk of attracting competitors and scavengers. A tendency to bite the neck or head of the prey is widespread among existing predators, including a variety of mammalian carnivores (Ewer 1968, 1973; Eaton 1970; Schaller 1972; Leyhausen 1973) and birds (Cade 1967; Scherzinger 1970; Ullrich 1971; Smith 1973), and experiments with hand-reared animals indicate that this may be an innate response (Leyhausen 1973; Lorenz & Leyhausen 1973; Smith 1973). The most important visual cues eliciting that response appear to be shape and motion of the prey. With respect to shape, experimental findings indicate that mammalian and avian predators tend to bite the most obvious constriction of the prey’s body—which is usually the region of the neck. With respect to movement, those predators tend to bite the ‘leading’ end of the prey—which is usually the head.

Palaeobiological evidence surveyed by Molnar & Farlow (1990) does not rule out the possibility that carnosaurs used prey-killing techniques comparable to those of existing big cats, which

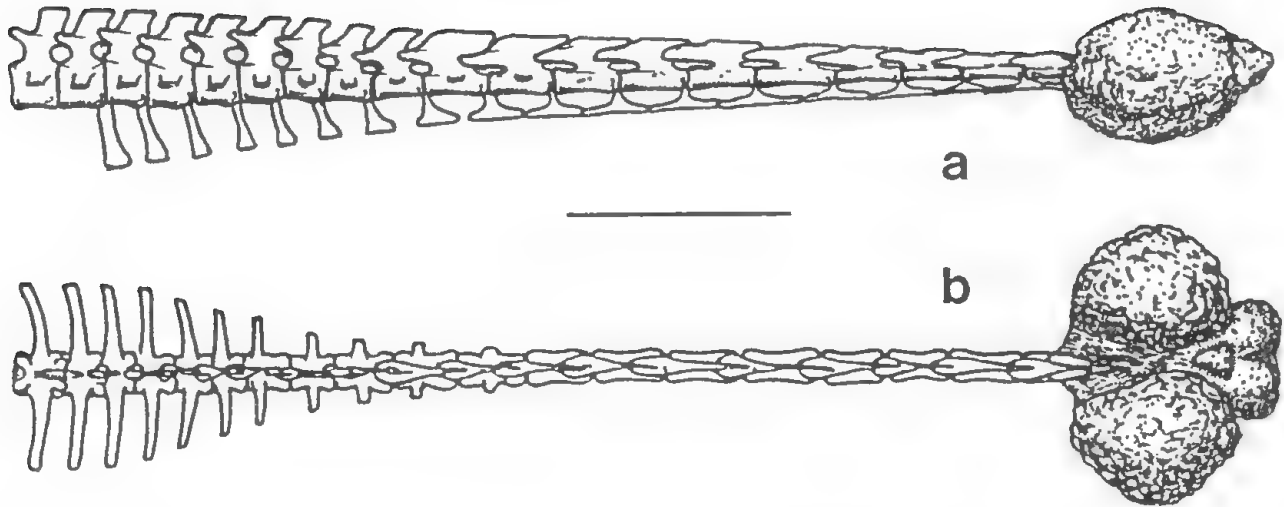


FIGURE 2. Tail skeleton of the ankylosaurid dinosaur *Euoplocephalus tutus*. **a**, Left lateral view. **b**, Dorsal view. Scale bar indicates 50 cm.

frequently employ a bite to the head or neck (Schaller 1967, 1972; Ewer 1973). This possibility does not imply that all carnosaurs adhered to a single pattern of prey-killing behaviour; rather, a tendency to seize the head or neck may be envisaged as a basic technique, which could have been modified (or even abandoned) to suit the circumstances of diverse carnosaurs.

It is noteworthy that many of the quadrupedal ornithischians susceptible to carnosaur attack (stegosaurs, ankylosaurids and nodosaurids) have a shallow skull that merges insensibly into a short neck. In effect, all these slow-moving herbivorous dinosaurs seem to have rendered the skull and neck as inconspicuous as possible. Among ankylosaurs there was also a tendency for the head and neck to be protected by a remarkable array of defensive structures. The head was encased in a veritable helmet of osteoderms, while the vulnerable region of the eye was shielded by a bony eyelid (Coombs 1972) and by an overhanging cornice of the skull roof. The shadow cast by this cornice may have concealed the eye, thus serving much the same role as a pigmented eye-stripe in many living animals (Cott 1940). In some ankylosaurs, such as the nodosaurid *Edmontonia rugosidens*, the neck was protected not only by its own covering of osteoderms but also by prominent bony spikes extending forwards from the region of the shoulder (Carpenter 1990, fig. 21.4; Coombs & Maryanska 1990, fig. 22.13). The existence of these elaborate defensive structures seems to confirm that the head and neck were particularly vulnerable regions of the ankylosaur body.

Theoretically, it is possible to test the suggestion that carnosaurs tended to attack the

head and neck of their prey: such behaviour might be expected to result in an unusually high incidence of teeth-marks on the neck and skull bones of animals killed by carnosaurs. Unfortunately, several factors conspire to render this test impracticable. First, it seems that predatory dinosaurs left surprisingly few teeth-marks on the bones of their prey (Fiorillo 1991). Second, teeth-marks in regions other than the head and neck would result from predators and scavengers dismembering carcasses and stripping them of their flesh. Next, some teeth-marks would be lost if bones were swallowed and partly or wholly digested by carnosaurs (Fiorillo 1991). And, finally, it is possible that the head of the prey was consumed preferentially, as among domestic cats and other small carnivores (Leyhausen 1973; Ewer 1968). For those reasons, the distribution and abundance of tooth-marks is unlikely to provide any clear indication to the prey-killing behaviour of carnosaurs. Moreover, it is unrealistic to assume that all carnosaurs shared a single pattern of prey-killing behaviour; instead, they probably exploited a repertoire of killing techniques (Molnar & Farlow 1990), each appropriate to the identity, size, weaponry and behaviour of particular prey animals. An analogous situation exists among mammalian carnivores, where an extensive range of prey-killing techniques appears to have been developed from the basis of a straightforward neck-bite (Ewer 1973).

HEADS AND TAILS

The heads and tails of ankylosaurids show

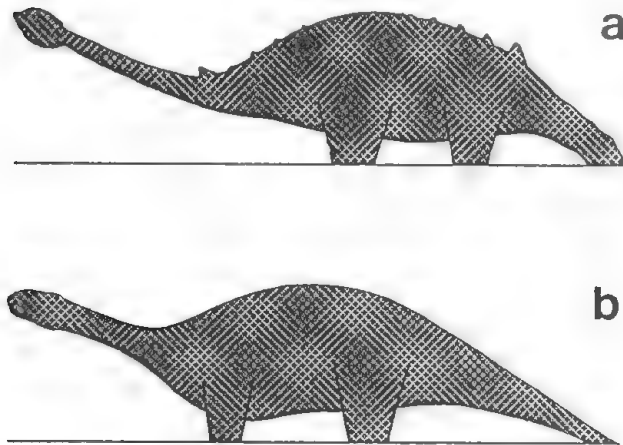


FIGURE 3. Silhouettes of dinosaurs, to illustrate potential role of ankylosaurid tail club as a 'dummy head'. **a**, The ankylosaurid dinosaur *Euoplocephalus tutus* (with head at right); feet and tip of snout are truncated, as if concealed by low vegetation, and the tail is raised. **b**, The ornithomimid dinosaur *Iguanodon* in quadrupedal posture (with head at left); tail is truncated, as if lying on the ground or concealed by vegetation.

divergent modifications in form: the head was rendered as inconspicuous as possible whereas the visual impact of the tail was exaggerated by the terminal club of bone. The net result is that head and neck resemble a smoothly tapering tail, whereas the tail has much the profile of a long neck and prominent head (Fig. 3). This unusual body outline calls to mind those insects that carry a conspicuous 'dummy head' at the rear end of the body (Fig. 4). Such dummy heads appear to divert predators away from the true head and towards the least vital extremity of the insect's body (Cott 1940; Wickler 1968; Edmunds 1974; Curio 1976). It is suggested here that the ankylosaurid tail club was an analogous dummy head that served to deceive predatory dinosaurs.

Before pursuing that suggestion, it must be noted that the term 'dummy head' (or 'false head') seems to have been applied indiscriminately to two rather different adaptations among living animals. Here I propose to separate 'dummy heads' into two categories—'duplicate' heads and 'substitute' heads. In some animals the head and tail are virtually identical in shape, as among amphispbaenians, snakes, typhlopids and certain scincid lizards. Here the tail duplicates the form of the head, or *vice versa* (Wickler 1968), thereby confusing and disorienting predators (Wickler 1968; Bustard 1969). In ankylosaurids, and their insect analogues, the tail appears to be modified as a visual substitute for the head (and *vice versa*), evidently serving to draw the attention of predators away from the true head. Here the substitute head

is more conspicuous than the true head. Although substitute heads may have originated through the elaboration of duplicate heads, the two adaptations are in many cases sufficiently distinct to warrant clear separation.

The substitute heads of ankylosaurids differ from those of insects in two important respects. First, the substitute head of an insect is disposable: its sacrifice may permit an insect to escape with minor damage (Cott 1940; Swynnerton 1926; Carpenter 1941). By contrast, the tail club of an ankylosaurid was not detachable. Second, insects can escape by jumping or flying, whereas ankylosaurids were probably incapable of outrunning theropod dinosaurs (Coombs 1978; Thulborn 1982, 1990). Ankylosaurids were obliged to stand and fight, and for that reason their substitute head is necessarily adapted as a robust deterrent weapon.

Insects possessing a substitute head often show appropriate peculiarities of behaviour (Cott 1940; Curio 1965, 1976; Wickler 1968). For instance, most butterflies rest head upwards on steep surfaces, but those with a substitute head

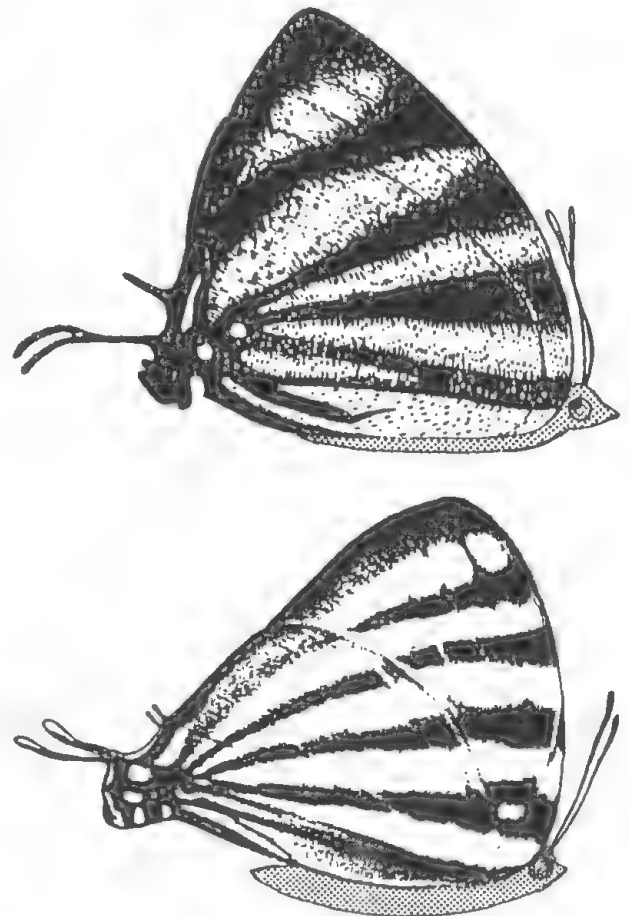


FIGURE 4. Butterflies of the genus *Thecla*, each with 'dummy head' (at left) bearing antenna-like filaments and eye-spot (adapted from Cott 1940; Wickler 1968).

frequently rest upside down. Butterflies of the species *Thecla togarna* instantly turn through 180° on alighting, so that the substitute head points in the previous direction of flight; then, on the approach of a predator, the butterfly appears to take off in the 'wrong' direction. In some cases the substitute head bears an eye-spot and antenna-like filaments whose movements simulate those of real antennae (Fig. 4), and butterflies of the genus *Deudorix* have been reported to walk backwards. Given these examples, it is conceivable that ankylosaurids equipped with a substitute head might also have indulged in some form of deceptive behaviour.

ANKYLOSAURID DEFENSIVE BEHAVIOUR

The foregoing analogies and constraints provide a framework for the following new model of ankylosaurid defensive behaviour.

In normal circumstances ankylosaurids probably carried the tail club at ground-level; it is unlikely to have been carried so conspicuously as to attract the attention of predators. On the close approach of a predator, the tail may have been raised to become clearly visible (Carpenter 1984; Fig. 3a). If a predator moved in to attack, appropriate movements of the ankylosaurid tail could simulate those of a genuine neck and head. On luring the predator within reach of the tail club, the substitute head might be swung away as if it were attempting to escape. This apparent retreat of the prey's head could provoke the predator into lunging after it, whereupon the tail club would be swung back straight into the face of the predator.

According to this model, ankylosaurids did not struggle to manoeuvre the tail club into a position suitable for striking an aggressor; instead, the aggressor was lured within reach of the tail club. Also, the tail club would strike at the aggressor's head, rather than its feet, thereby achieving the greatest deterrent effect. The model requires that an aggressor should respond to the two most important visual cues known to affect the behaviour of existing predators: movement (the apparent 'escape' of the prey's 'head') and shape (the sharp constriction behind the prey's 'head'). Finally, a tail club disguised as a head would permit an ankylosaurid to deal with two or more predators, as each of them would fall prey to the same deception.

This model finds similarities in the defensive adaptations of certain molluscs and beetles. Many

colloid molluscs have vividly coloured dorsal papillae, which may be erected and waved about on the approach of an aggressor (Edmunds 1966, 1974). The papillae contain nematocysts, as predators may discover to their cost. However, it is not clearly established that the papillae simulate items of prey, nor that their movements serve in distracting and luring predators; the papillae might equally well be interpreted as aposematic devices (Cott 1940). Similar uncertainties apply in the case of those carabid beetles that squirt an acid secretion from the tip of the tail. Although prominent white eye-spots may divert predators to the tail of the beetle (Marshall & Poulton 1902), these might, once more, be aposematic in function. In view of these uncertainties, it is impossible to identify any extant organism that duplicates the entire pattern of defensive behaviour proposed for ankylosaurids. Nevertheless, every component of that behavioural model has some counterpart among living organisms. For example, both snakes and cats are known to lure or distract other animals by twitching the tip of the tail (Wickler 1968; Carpenter & Ferguson 1977).

MIMICRY?

If the ankylosaurid tail club did function as a substitute head, it would probably qualify as an example of mimicry. Certainly, it would exemplify Wickler's concept of mimicry (1965, 1968), which required the deception of a signal-receiver (usually a predator). The more restrictive definition proposed by Vane-Wright (1976) placed no emphasis on deception, but depended instead on the outcome of interactions between the mimic, its model and the signal-receiver. Vane-Wright specifically excluded 'decoys and deflective marks', including dummy heads, from the realm of mimicry. However, the ankylosaurid tail club may have been multifunctional – serving in turn as a deflective structure, a lure and a weapon. In performing the second of those functions, by luring an aggressor within reach, the tail club would merit inclusion in Vane-Wright's category II (synergic aggressive mimicry). The requirements of this category are: (1) that the mimic simulates an organism attractive to the signal-receiver, and (2) that on the signal-receiver's approach, the mimic interacts with it to the advantage of the model. In the case of ankylosaurids, the tail would simulate the generalized form of head and neck in other ornithischian dinosaurs (most obviously the

ornithopods, Fig. 3b). Those other ornithischians would derive advantage, in Vane-Wright's words (1976: 36), 'through the removal or debilitation of their predators'.

Such interpretation of the ankylosaurid tail club constitutes the first report of mimicry in dinosaurs. Although a tail club occurred in at least two genera of sauropod dinosaurs (Dong *et al.* 1989), this was comparatively small and might not have been functionally equivalent to that of ankylosaurids. Even so, the defensive model proposed for ankylosaurids might be extrapolated to certain stegosaurs, where conspicuous tail spikes (see Galton 1990) may have drawn the attention of predators before being employed as a deterrent weapon.

DISCUSSION

Mimicry is a subject of enduring controversy among biologists. Wickler remarked (1968: 13) that 'one hundred years after Bates [1862] first clearly defined the concept of mimicry, a review of the literature listed 1 500 papers arguing for or against it. This amounts to roughly fifteen papers a year, or more than one a month.' Few examples of mimicry have been identified among vertebrate animals (Wickler 1968: 18), and not surprisingly this phenomenon is virtually unknown in the fossil record (Boucot 1990: 457). In these circumstances the foregoing hypothesis of mimicry in ankylosaurid dinosaurs might be regarded with some scepticism. It seems appropriate to examine two predictable objections to that hypothesis.

First, it may be objected that hypotheses about the behaviour of extinct organisms are not amenable to scientific testing. In the present case it is difficult to imagine how the behavioural interactions of ankylosaurids and their predators could ever be corroborated or falsified. Although this objection is certainly valid, it does not necessarily condemn the proposed model of ankylosaurid defensive behaviour to the realm of unscientific speculation. That model meets the stringent requirements of a scientific hypothesis in two respects—congruence and productivity.

With regard to congruence (or consilience), the model provides a single coherent explanation for all pertinent observations, particularly those concerning the anatomical peculiarities of ankylosaurids. By contrast, one conventional interpretation of ankylosaurid defensive behaviour involves a major inconsistency or internal contradiction: it requires that the ankylosaurid

body plan should confer both great stability and a high degree of agility. To use a familiar analogy, that conventional interpretation requires that ankylosaurids should combine the stability of a four-wheel-drive vehicle with the turning circle and manoeuvrability of a motor-cycle. (Alternatively, one might try to envisage a single human possessing both the stability of a Sumo wrestler and the agility of a ballet dancer.) Such a combination of antagonistic physical properties may well be an unattainable ideal and it appears to be approached only in exceptional circumstances (e.g. in the case of a tank, or a bulldozer, with one caterpillar tread operating in reverse). Although there is a suggestion that stegosaurs were capable of fending off predators by pivoting very rapidly on the hindfeet alone (Bakker 1986), it seems much less likely that the broad-bodied ankylosaurids could have done so.

The model proposed in this paper meets the requirement for productivity by generating predictions that are (in theory at least) scientifically testable. One such prediction, concerning the distribution of teeth-marks left by predatory dinosaurs, was mentioned earlier. Two more predictions, derived from the general principles of mimicry, are: (a) that the mimics (ankylosaurids) should have inhabited the same environments as their models (ornithopods), and (b) that the mimics should have been less abundant than their models (Wickler 1968: 46–48). Yet another prediction stems from the suggestion that a substitute head may originate through the elaboration of a duplicate head: consequently, one might expect the ancestors of ankylosaurids to have possessed a tail that was similar in size and overall shape to the head and neck combined. By contrast, conventional interpretations of ankylosaurid defensive behaviour seem to generate only a single prediction—namely, that the lower leg and ankle were those regions of the carnosaur body most likely to sustain injuries during encounters with ankylosaurids. The model proposed in this paper offers a conflicting prediction—that such injuries were more likely to affect the carnosaur skull.

Second, it might be objected that the ankylosaurid tail bears only slight resemblance to the head and neck of an ornithopod, and that such a remote similarity would be unlikely to deceive a discriminating predator. This objection encapsulates the common belief that a successful mimic must show close and detailed resemblance to its model, on the assumption that some less exact resemblance to the model would be

inadequate to deceive a signal-receiver. Similar assumptions were adopted by Punnet (1915) and Goldschmidt (1945), who maintained that mimicry could not arise through gradual processes of natural selection because the initial chance resemblance between mimic and model would be so slight as to confer no advantage. However, this assumption appears to be groundless: experimental studies with birds, insects and artificial models reveal that some mimics can, and do, derive advantage from only superficial similarity to their models (Duncan & Sheppard 1965; Wickler 1968: 94; Edmunds 1974: 90–99). For instance, Brower *et al.* (1963: 80) stated 'as an experimentally demonstrated fact ... that even a remote resemblance between heliconiine butterflies can be advantageous' in conferring protection from predators. Moreover, it cannot be assumed that all predators are equally discriminating. Among birds, for example, the situation was summarized by Edmunds (1974: 92) as follows:

it is likely that a whole spectrum exists from birds which recognize prey by a single visual cue, and are hence easily deceived by even a poor mimic, to birds which recognize prey by overall appearance or by many visual cues and which can distinguish almost perfect mimics from their models.

It is possible that a similar spectrum existed among theropod dinosaurs, with some identifying their prey by means of its overall appearance (*Gestalt* perception) while others relied on one or more specific visual cues, such as shape and direction of movement. The less discriminating of those predatory dinosaurs might well have been deceived by ankylosaurids equipped with a dummy head.

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EMYDURA LAVARACKORUM, A NEW PLEISTOCENE TURTLE (PLEURODIRA : CHELIDAE) FROM FLUVIATILE DEPOSITS AT RIVERSLEIGH, NORTHWESTERN QUEENSLAND

A. W. WHITE AND M. ARCHER

Summary

In 1986 the carapace, plastron and pelvic remains of a large chelid turtle were recovered from Pleistocene sediments on Riversleigh Station in northwestern Queensland. The fossil remains are described herein. The good state of preservation enabled the remains to be placed in an extant genus (*Emydura*) within the Chelidae on the basis of a derived feature of the carapace. Distinctive features such as wide bridge, broad first vertebral scute, unusual epiplastrahypoplastron suture, thickened bridge, buttresses and deep intergular insertion between the humerals prevent these fossils from being assigned to a known species. Accordingly, a new species of *Emydura* is proposed and comparisons are made between it and the currently recognised congenors.

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A. W. WHITE AND M. ARCHER

WHITE, A. W. & ARCHER, M. 1994. *Emydura lavarackorum*, a new Pleistocene turtle (Pleurodira: Chelidae) from fluvial deposits at Riversleigh, northwestern Queensland. *Rec. S. Aust. Mus.* **27**(2): 159–167.

In 1986 the carapace, plastron and pelvic remains of a large chelid turtle were recovered from Pleistocene sediments on Riversleigh Station in northwestern Queensland. The fossil remains are described herein. The good state of preservation enabled the remains to be placed in an extant genus (*Emydura*) within the Chelidae on the basis of a derived feature of the carapace. Distinctive features such as a wide bridge, broad first vertebral scute, unusual epiplastral-hyoplastron suture, thickened bridge buttresses and deep intergular insertion between the humerals prevent these fossils from being assigned to a known species. Accordingly, a new species of *Emydura* is proposed and comparisons are made between it and the currently recognised congeners.

Arthur W. White and Michael Archer, School of Biological Sciences, University of New South Wales, P.O. Box 1, Kensington, New South Wales, 2033. Manuscript received 17 September 1993.

Chelid fossil shell fragments are common in the Pliocene–Pleistocene deposits throughout Australia (e.g. in the Pliocene and Pleistocene deposits of the Darling Downs; Molnar 1982) but few are sufficiently complete to permit a detailed comparison with the shells of living species (Gaffney 1981).

In May, 1984 exploration of eroded fluvial deposits exposed in the watershed of the Gregory River on Riversleigh Station, northwestern Queensland, revealed several sites that produced fossil vertebrates. One of these, now known as Terrace Site, produced abundant remains of chelid turtles as well as the Pleistocene marsupial *Diprotodon optatum*, unidentified macropodoids, murids, crocodilians, lacertilians, fish and invertebrates (bivalves and gastropods). Preliminary accounts of the discovery of Terrace Site have been given in Archer, Hand and Godthelp (1986).

From approximately 30 cm above the base of the palaeochannel, in a layer with abundant bivalves and mammal bone fragments, a nearly complete although somewhat crushed chelid shell was recovered. It is sufficiently well preserved to enable comparison with a wide range of living chelids and is the basis for the species described herein.

Additional vertebrate remains from this deposit will be reported elsewhere (Godthelp, in

preparation; Willis and Archer 1990; Willis, in preparation).

The anatomical terminology used in this paper follows that employed by (Gaffney 1977). That of modern chelid taxonomy follows Cogger (1993) and Obst (1986). Qualitative and quantitative methods of analysis follow Auffenberg (1976).

METHODS

After being exposed in the deposit, the specimen was hardened with aquadhere, braced and secured in a plaster jacket. In the laboratory, various sections of the shell, defined by post-depositional crushing, were reconstructed using aquadhere. Measurements were made with dial calipers to the nearest millimetre.

Measurements and abbreviations used here are as follows:

Carapace

Anterior Carapace Width (ACW) = the anterior width of the carapace measured from the most anterior points of the $M_2 - M_3$ sutures.

Width of V_1 (V_1W) = the maximum width of the first vertebral scute.

Length of V_1 (V_1L) = the maximum length of the first vertebral scute.

Width and Length of Subsequent Scutes (Indicated by the appropriate subscript).

Length of C_1 (C_1L) = the maximum length of the first costal scute.

Plastron

Total Plastron Length (TPL) = measured in parallel to the midline from the most anterior to most posterior part of the plastron.

Anterior Plastron Length (APL) = measured in parallel to the midline from the most anterior portion of the plastron to the anterior margin of the bridge.

Bridge Width (BW) = the width of the bridge at the junction of the plastron.

Posterior Plastron Length (PPL) = measured in parallel to the midline from the most posterior portion of the plastron to the posterior margin of the bridge.

Intergular Width (IW) = the width of the intergular measured along the anterior margin of the plastron.

Intergular Length (IL) = the maximum length of the intergular scute.

Gular Width (GW) = the width of the gulars along the anterior margin of the plastron.

Gular Length (GL) = length of the gular-intergular suture.

Intergular Insertion (II) = the distance along the midline that the intergular scute penetrates between the humeral scutes i.e. measured from a line level with the posterior ends of the gulars to the posterior end of the intergular.

Humeral Length (HL) = the length of the humeral scutes along the midline.

Pectoral Length (PL) = the length of the pectoral scutes along the midline.

Abdominal Length (AL) = the length of the abdominal scutes along the midline.

Femoral Length (FL) = the length of the femoral scutes along the midline.

Anal Length (AnL) = the length of the anal scutes along the midline.

Anal Width (AW) = the distance between the most posterior parts of the opposing anal scutes.

Epiplastron Length (EpL) = the length of the epiplastron bones along the midline.

Entoplastron Length (EnL) = the maximum length of the entoplastron.

Entoplastron Width (EnW) = the maximum width of the entoplastron.

Hypoplastron Length (HyL) = the length of the hypoplastron bones along the midline.

Comparative Specimens Examined

Many of the comparative specimens of modern species examined during this study are lodged in the herpetological collections of the Australian Museum as follows:

Emydura australis: R20737, R72786, R72787.

Emydura krefftii: R14925.

Emydura macquarii: R1188, R6789, R81477, R85727, R104335, R123049

Emydura novaeguineae: R5042, R24460.

Emydura signata: R58588, R58589, R96716.

Elseya dentata: R3699, R3700, R31728, R36998, R40181,

Elseya latisternum: R20330–20345, R21224, R21485, R21570–21572, R37657–37665, R43530, R43542, R81958.

Rheodytes: R125481

Other specimens of these species were examined from the authors' collections. A specimen of *Pseudemydura umbrina* was examined from the Western Australian museum (WAM 13744). A specimen of the alpha taxon turtle was examined from John Cann's collection.

SYSTEMATICS

Order: Testudines Linneus, 1758

Infraorder: Pleurodira (Cope, 1868)

Family: CHELIDAE Gray, 1825

Genus: *Emydura* Bonaparte, 1836

Emydura lavarackorum White & Archer n. sp.
(Figs 1,2,3 and 4)

Holotype:

Queensland Museum Palaeontological Collections no. F 24121, an associated almost complete plastron, partial carapace and pelvic fragments collected 9th May, 1986, by J. and S. Lavarack.

Type locality and age:

Terrace Site, an excavation in fluvial sediments exposed on the south bank of the Gregory River, Riversleigh Station, northwestern Queensland, approximately 200km northwest of Mount Isa. More precise locality data are recorded and may be available on application to the Queensland Museum or the University of New South Wales. The presence in the sediments of material referable to *Diprotodon optatum* and no

other index fossil indicative of any other period of time is the basis for interpreting the deposit to be Pleistocene in age. No more precise age determination is available at this time although samples suitable for radiocarbon dating have been collected.

Diagnosis:

This species differs from all others in the following combination of features. The first

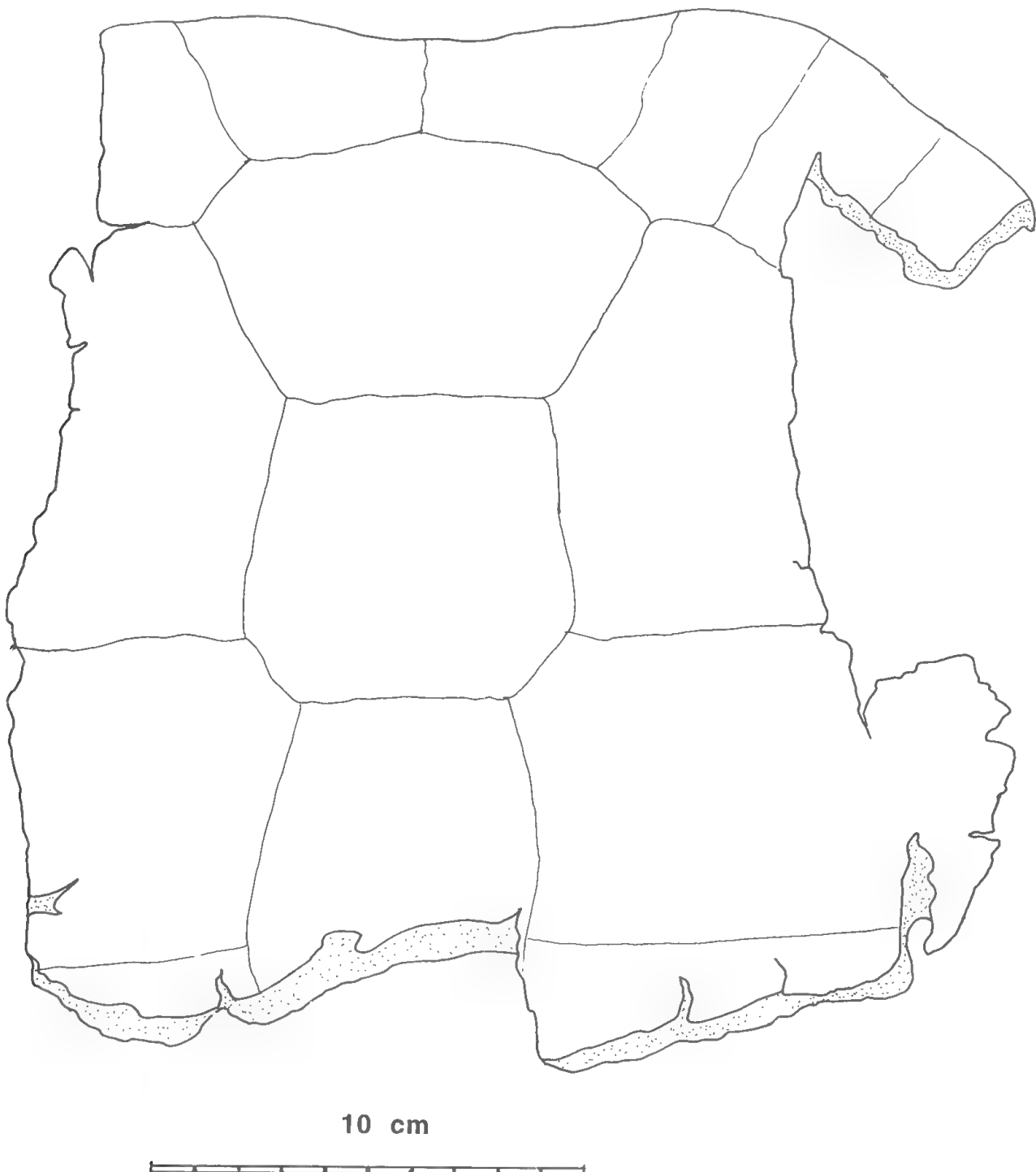


FIGURE 1. Dorsal view of anterior carapace of *Emydura lavarackorum*.

vertebral scute (V_1) is much wider than V_2 . Vertebral scutes V_2 and V_3 are rectangular, being longer than they are broad, with very small projections into the costal junctions (Fig. 1). The humeral-pectoral seam is sigmoidal rather than straight. The anterior straight edge of the carapace is wide and incorporates the two left and right marginal scutes (before the carapace curves posteriorly). The anterior bridge struts are unusually thick. The anterior edge of the gular is as wide as the anterior edge of the intergular. The intergular is long and deeply divides the humeral

scutes. The intergular intrusion between the humerals is greater than the gular length. The intergular scutes narrow at the anterior edge of the carapace. The bridge is broad ($BL:TPL = 0.29$). The acetabulum is circular and is contributed to equally by all three pelvic bones. The acetabulum has a diameter of 25 mm. The upper (ilial) lip of the acetabulum is raised and overhanging whereas the lower lip (ischium and pubis) is less pronounced.

Etymology:

The species name is in honour of Sue and Jim Lavarack, hard-working volunteers who, besides having collected the holotype (Archer 1988) and supervised excavations at Terrace Site for five years, have maintained a continuous supportive role in the work done at Riversleigh and on Riversleigh materials which they have helped to prepare in Sydney.

Description:

The plastron is long (390 mm) and almost complete except for some medial gaps in the anal region (Fig. 2). The plastron is evenly rounded at its anterior end. The posterior end of the plastron terminates with two pointed anal projections. The anterior lobe of the plastron is broader (maximum width 165 mm) than the posterior lobe (maximum width 154 mm).

The endoplastron is wider ($EnW = 58$ mm) than it is long ($EnL = 45$ mm) (Fig. 3). The epiplastral-hypoplastral suture is sigmoidal. The hypoplastra are the longest bony elements in the plastron ($HyL = 105$ mm). Of the epidermal scutes, the intergular is the most distinctive. It completely separates the gulars and penetrates deeply between the humerals. The humeral-humeral seam is only 15 mm long whereas the humerals have a maximum height of 87 mm. The longest scutes are the abdominal ($A_1 = 105$ mm), followed by the femoral scutes ($F_1 = 95$ mm), pectoral scutes ($PL = 67$ mm), anal scutes ($AnL = 66$ mm), intergular ($IL = 62$ mm) and finally the humerals ($HL = 15$ mm).

The humeral-pectoral seam is sigmoidal, the most anterior sections being at the midline and at the extreme margins. The intergular has a maximum width of 26 mm but is only 19 mm wide along the anterior edge of the plastron. The gulars are small being only a little wider ($GL = 28$ mm) than the intergular. The intergular extends most of the way between the humerals. The intergular intrusion is longer than the gular length.

The carapace is large and flat along the ventral surface. The leading edge of the carapace is almost

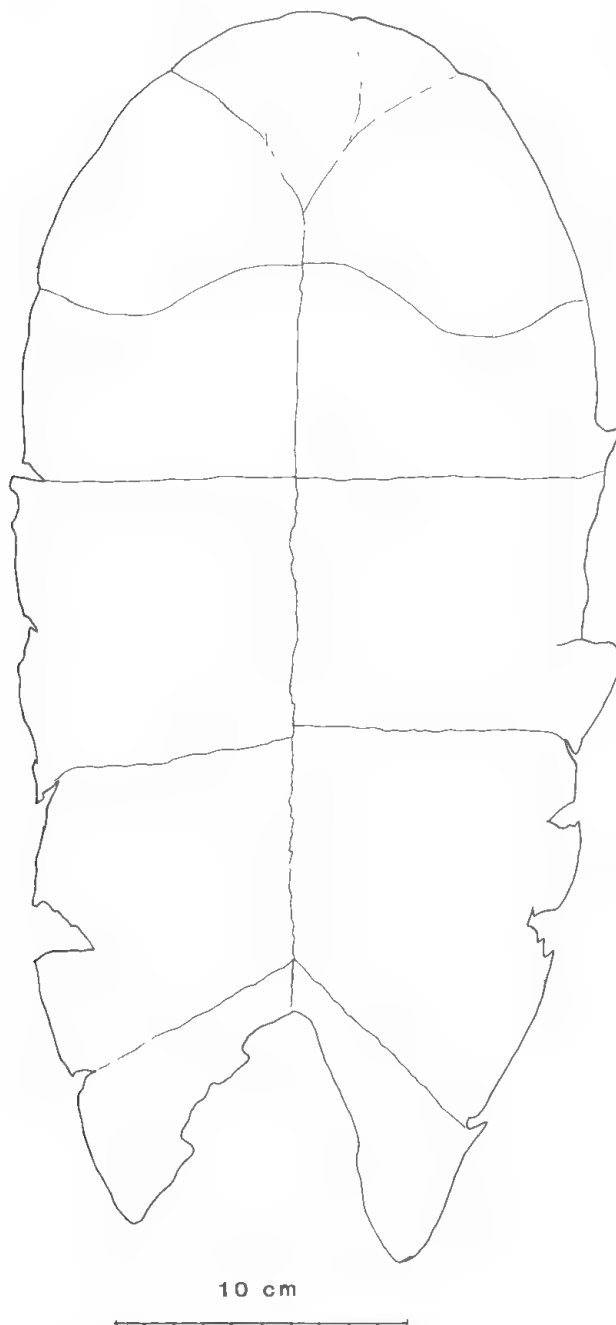


FIGURE 2. External view of plastron of *Emydura lavarackorum*

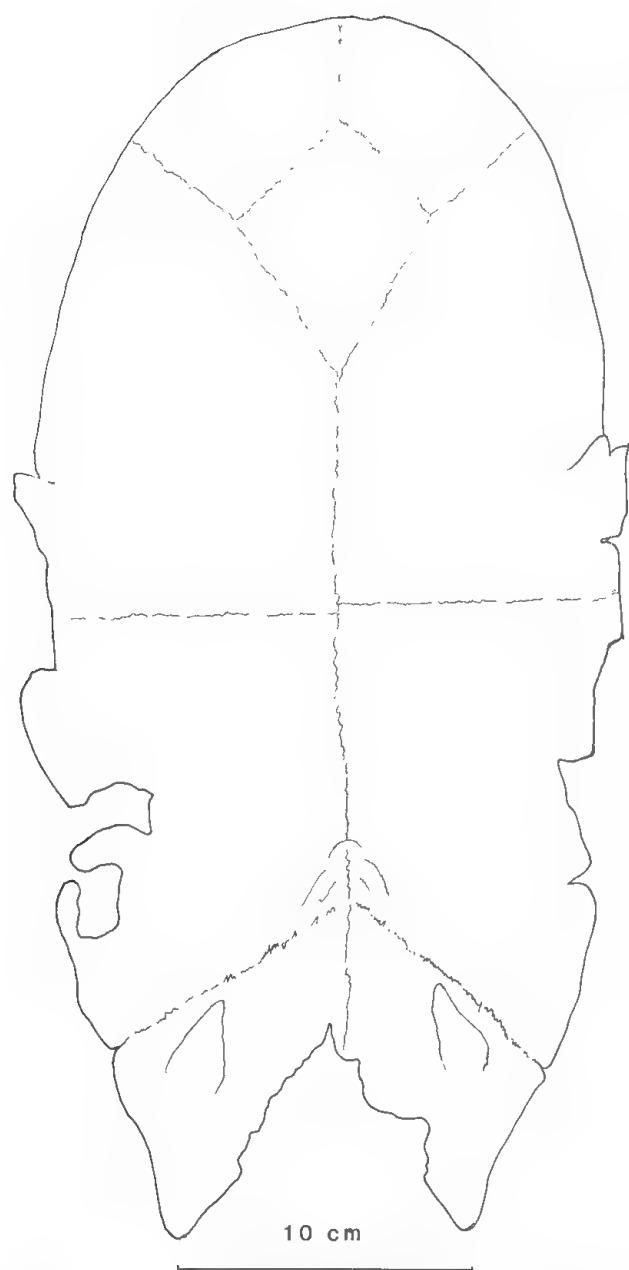


FIGURE 3. Internal view of plastron of *Emydura lavarackorum*.

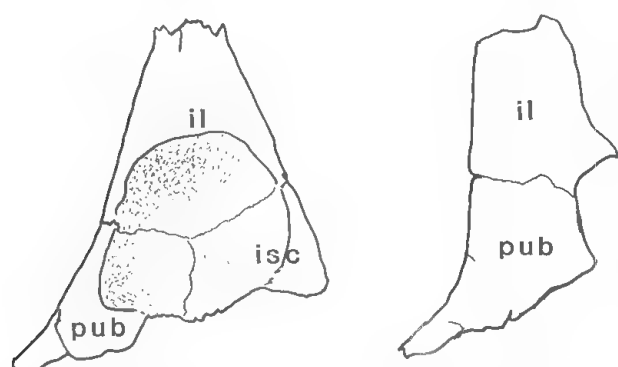


FIGURE 4. Acetabular view and lateral view of the left hip of *Emydura lavarackorum*.

straight and does not curve posteriorly until the suture line between the second and third marginal scutes. A precentral (nuchal) scute is absent. The broad anterior edge of the carapace is reflected by an expansion of the V_1 scute (maximum width 103 mm). This scute is almost twice as wide as the second vertebral scute (width 56 mm). V_1 (height 70 mm) is not as high as V_2 (height 87 mm). The third vertebral scute is incomplete but appears to be of similar proportions to the V_2 scute. The projections of the vertebral scutes between the costals is minimal. The first costal scute (C_1) is higher (95 mm) than C_2 (83 mm in height). It was not possible to measure the width of the costals.

The recess for the insertion of the anterior bridge strut on the undersurface of the carapace is steeply angled across the first pleural bone and is not in line with the raised process that forms the mid-pleural wall. The recess abuts the second peripheral bone and forms most of the base of the third peripheral (Fig 5). The dorsal fork of the transverse process on the first thoracic vertebra sweeps backwards to form the top of the mid-pleural wall.

A major section of the left pelvis comprising of the ischium, ilium and pubis was measured. The piece was 55 mm long and 20 mm wide at the ilial fracture. It was 35 mm wide at a position level with the acetabulum (which had a diameter of 25 mm).

The acetabulum is quite deep and is overhung by a pronounced upper ridge formed by the extension of the ilial ridge (Fig 4). The lower lip of the acetabulum has a much weaker rim formed a joining ridge continuous between the pubis and ischium.

Measurements (mm) of the holotype:

ACW = 210; V_1 W = 105; V_1 H = 72; V_2 W = 65; V_2 H = 87; C_1 H = 95; C_2 H = 83; TPL = 390; APL = 110; BW = 115; PPL = 165; IW = 20; IH = 62; GW = 30; GL = 30; II = 36; HL = 15; PL = 67; AL = 105; FL = 95; AnL = 66; AW = 93; EpL = 30; EnH = 45; EnW = 58; HyL = 105.

COMPARISONS AND DISCUSSION

The Riversleigh fossil turtle is placed in the Chelidae because of the evidence of pelvic fusion to the shell and the absence of mesoplastra and neural bones (Gaffney 1977).

Within the Chelidae, the Riversleigh turtle is placed in the genus *Emydura* on the basis of a recently identified synapomorphy. This feature relates to the insertion of the anterior bridge into

TABLE 1. Shell characteristics of Australian short-necked chelids.

Feature	<i>Rhedytes</i>	<i>Alpha</i>	<i>Elseya dentata</i>	<i>Elseya latisternum</i>	<i>Emydura krefftii</i>	<i>Emydura macquarii</i>	<i>Pseudemydura</i>
Relative Length of Anterior Plastron	60-70% of the length of the posterior plastron	66% of the length of the posterior plastron	80-90% of the length of the posterior plastron	82-95% of the length of the posterior plastron	75-88% of the length of the posterior plastron	75-85% of the length of the posterior plastron	45-65% of the length of the posterior plastron
Relative Width of Anterior Plastron	Narrower than the posterior plastron	Wider than the posterior plastron	Narrower than the posterior plastron	Wider than the posterior plastron	Wider than the posterior plastron	Wider than the posterior plastron	Wider than the posterior plastron
Bridge Width	Narrow: shorter than the length of ant. plastron	Narrow: shorter than the length of ant. plastron	Broad: longer than the anterior plastron	Narrow: shorter than length of ant. plastron	Broad: longer than the anterior plastron	Broad: longer than length of ant. plastron	Broad: longer than length of ant. plastron
Bridge Buttresses	Pronounced inguinal and axillary buttressing	Pronounced inguinal and axillary buttressing	No raised buttressing	No raised buttressing	No raised buttressing	No raised buttressing	No raised buttressing
Shape of Recess for Anterior Bridge Struts	Recess in line with mid pleural wall	Recess in line with mid pleural wall	Recess in line with mid pleural wall	Recess in line with mid pleural wall	Recess angled above mid pleural wall	Recess angled above mid pleural wall	Recess in line with mid pleural wall
Relative Width of Intergular	Narrower than the gulars	Narrower than the gulars	Narrower than the gulars	Wider than the gulars	Narrower than the gulars	Narrower than the gulars	Wider than the gulars
Extent of Gular Penetration	Intergular penetrates 1/3 between humerals	Intergular penetrates half way between gulars	Intergular penetrates half way between humerals	Intergular penetrates half way between humerals	Virtually no separation of humerals by intergular	Intergular penetrates half way between the humerals	Intergular complete

the ventral surface of the carapace. The recess for the anterior bridge is angled steeply backwards to reach the raised process that forms a transverse wall across the floor of the first pleural bone. In the other chelid genera, the recess is itself transverse and so forms a near continuous line with the mid-pleural wall (Fig. 5). The Riversleigh *Emydura* has this derived characteristic.

Osteological comparisons (e.g. Gaffney 1977) of the shells and skulls of *Emydura* and *Elseya* have highlighted the great degree of similarity between these two genera. Current taxonomy (Obst 1986, Cogger 1993) recognises two species of *Elseya* and 6 species of *Emydura*. The diagnostic features that are used to identify the genera and species are features that include soft anatomy, skull ridges and plastral scute patterns. Legler (1985) and Georges and Adams (1993) have cast doubts about the validity of current concepts of these genera, especially *Elseya* which appears to be paraphyletic. On the basis of the carapacial synapomorphy identified in this paper *Emydura*, however, appears to be monophyletic.

The Riversleigh *Emydura* is a large turtle compared to other Australian chelids. It has a plastral length of 39 cm and hence would most likely have had a carapace length of approximately 41 cm. In comparison, the largest measured extant chelid is *Elseya dentata*. Cann (1986) has reported adults of this species with carapace lengths of up to 36.5 cm. The largest *Emydura* species is *E. macquarii* which may reach shell lengths of up to 40 cm (Cogger 1993).

In the extant Australian chelid species, the bridge typically occupies between 20 and 30% of the plastron length (Table 1). *Emydura macquarii* and *E. signata* have the narrowest bridge (20–23% of the plastron length) of all *Emydura*

species. In contrast the bridge of *E. krefftii* is particularly broad and varies between 28 and 33% of the plastron length. In the Riversleigh turtle, the bridge is wide (30% of the plastron length).

The bridge struts of the Riversleigh turtle are unusually thick. The anterior bridge struts are 2.15 cm wide at the base and almost 1 cm wide in the middle. The largest comparative chelid specimen that was available for measurement was a deep-shelled snapper (*E. dentata* carapace length 28.5 cm, R40181). The anterior bridge strut of this animal was only half as massive.

Carapace shape varies in *Emydura*. Species such as *E. macquarii* and *E. signata* have broad, low domed carapaces that are expanded at the rear. In the range of shell shapes *E. krefftii* represents the other extreme and has a high domed carapace that is not expanded at the rear (Goode 1966). *E. lavarackorum* is intermediate in shell shape and has a carapace that is not evenly rounded.

In all species of *Emydura* the gular scutes of the plastron are completely divided by the intergular (Table 1). *Emydura* turtles also show partial separation of the humerals by the intergular, with the degree of separation being less than half of the mid-humeral length. Of the other Australian chelid genera, only in *Pseudemydura* does the intergular also completely divide the humerals. The intergular of *Elseya latisternum* produces the weakest separation of the humerals and barely intrudes between the humerals. *Emydura lavaracki* is most distinctive in this regard as the intergular deeply divides the humerals without completely separating them.

In the extant Australian *Emydura*, the arrangement of the pelvic bones around the acetabulum is similar. Here the ilium, ischium and

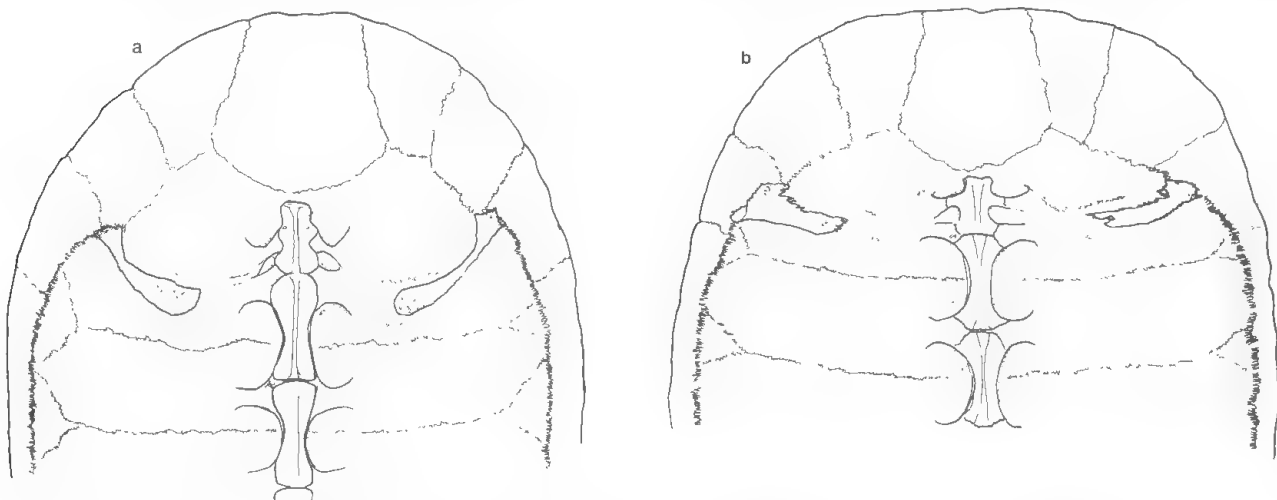


FIGURE 5. View of the undersurface of the anterior carapaces of *Emydura krefftii* (a) and *Elseya latisternum* (b).

pubis contribute almost equally to the composition of the acetabulum. This arrangement is also present in *Emydura lavarackorum*. In the extant species of *Emydura* the upper and lower rim of the acetabulum are equally protuberant. *E. lavaracki* is different in this regard as the upper lip of the acetabulum is more substantial than the lower lip. This means that the acetabulum is relatively deeper in this species.

The conventional guide for determining species within the genus *Emydura* is based on features of soft anatomy, shell shape and distribution (Cogger 1993). Other shell features have been used such as the relative length of the plastron compared to the carapace, the relative length of the anterior plastron compared to the posterior plastron and the relative width of the bridge (Goode 1966). *E. macquarii* has a plastron that is noticeably shorter than the carapace (80–85% of the carapace length). By way of contrast, *E. krefftii* has a longer plastron that ranges from 85–95% of the carapace length. Based on the shell reconstruction of *E. lavarackorum* the plastron appears to be about 95% of the length of the carapace. In some species of *Emydura*, such as *E. macquarii*, the anterior plastron is conspicuously shorter than the posterior plastron. In comparison, *E. krefftii* has anterior and posterior plastron segments that are almost equal in length. *E. lavarackorum* the anterior plastron is much shorter (67%) than the posterior plastron.

In view of the many evidently significant differences between the Riversleigh fossil species and any others referred to this genus, we have no hesitation in describing the fossil form as the new species *Emydura lavarackorum*.

Although we have placed this species in the genus *Emydura* on the basis of shell morphology it is apparent that it is not particularly closely related to any of the other species in this genus. In two respects, this Pleistocene chelid is unlike all

Australian short-necked turtles: the massive expansion of the V_1 scute and the deep extension of the intergular between the humerals. In these features, the Riversleigh form more closely resembles the long-necked chelids. Further clarification of the intrafamilial affinities of the Riversleigh form may have to await discovery of cranial material.

ACKNOWLEDGMENTS

We wish to acknowledge the vital financial support the Riversleigh Project has had from: the Australian Research Grant Scheme (Grant PG A3 851506P); the National Estates Scheme (Queensland); the Department of Environment and Arts; Wang Australia Pty Ltd; ICI Australia Pty Ltd; the Queensland Museum; the Australian Geographic Society; Mount Isa Mines Pty Ltd; and Surrey Beatty & Sons Pty Limited. Critical logistical support in the field and laboratory has been received from the Riversleigh Society, the Friends of Riversleigh, the Royal Australian Air Force, the Australian Defence Force, the Queensland National Parks and Wildlife Service, the Riversleigh Consortium (Riversleigh being a privately owned station), the Mount Isa Shire, the Burke Shire, the Northwest Queensland Tourism and Development Board, the Gulf Local Development Association, PROBE and many volunteer workers and colleagues including Dr Suzanne Hand and Henk Godthelp who helped to recover the holotype. Alan Rackham Snr and Alan Rackham Jnr discovered the Terrace Site in the first place. Among the volunteers who helped at the 1984 Riversleigh Expedition, special thanks are extended to Bruce Armitage, John Courtenay, Martin Dickson, Joy Dohle, Archie Daniels, Bernie Jennings, Leslie Hobbs, Bill Lockwood, Audrie and Harry Macintosh, Reg Markham, Melody Nixon, Ron Norman, Jim and Sue Lavarack, Brian, Bronwen and Dan O'Dwyer, Lazar Radanovich, Jim Ross, Mary Sandilands, Donald and Sue Scott-Orr, Jack Struber, Dr Steven Waite and Shirley Webster.

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FROGS FROM A PLIO-PLEISTOCENE SITE AT FLORAVILLE STATION, NORTHWEST QUEENSLAND

MICHAEL J. TYLER, HENK GODTHELP & MICHAEL ARCHER

Summary

Six frog ilia, mostly in good condition, have been recovered from riverine granuals on the western bank of the Leichhardt River, south of the Floraville Station in northwest Queensland.

FROGS FROM A PLIO-PLEISTOCENE SITE AT FLORAVILLE STATION, NORTHWEST QUEENSLAND

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TYLER, M. J., GODTHELP, H. & ARCHER, M. 1994. Frogs from a Plio-Pleistocene site at Floraville Station, northwest Queensland. *Rec. S. Aust. Mus.* **27**(2): 169–173.

Six frog ilia, mostly in good condition, have been recovered from riverine gravels on the western bank of the Leichhardt River, south of the Floraville Station Homestead at Floraville Station in northwest Queensland.

Three species of frogs are included: the extant species *Cyclorana cultripes* Parker, *C. platycephala* (Günther) and also *Limnodynastes* sp. cf. *L. tasmaniensis* Günther. They constitute the first fossil record of the fossorial genus *Cyclorana*, whilst the *Limnodynastes* species resembles closely material from earlier (Oligo-Miocene) sites at the nearby locality of Riversleigh Station.

M. J. Tyler, Department of Zoology, University of Adelaide, South Australia 5005, and H. Godthelp and M. Archer, Vertebrate Palaeontology Laboratory, School of Biological Sciences, University of New South Wales, Kensington, New South Wales 2006. Manuscript received 12 May 1993.

A characteristic of the frog fossil record in Australia is that most of the Tertiary sites are in the north of the continent, whereas the Quaternary sites are predominantly in the south (Tyler, 1989, in press; Tyler & Godthelp, 1993). Here we report an exception to the trend, for one of us (M. A.) recovered vertebrate material from an undated site in northwest Queensland considered to be Plio-Pleistocene. The site was named 5C in the M. A. notebook and consists of riverine gravels located on the western bank of the Leichhardt River south of the Floraville Station Homestead. Included are six anuran ilia representing three species.

MATERIALS AND METHODS

The ilia are deposited in the collection of the Queensland Museum, Brisbane. Methods of measurement and descriptive terminology follow Tyler (1976). Scanning electron micrographs were prepared with a Cambridge Autoscan Model 5250.

SYSTEMATICS

Family HYLIDAE

Sub-family PELODRYADINAE

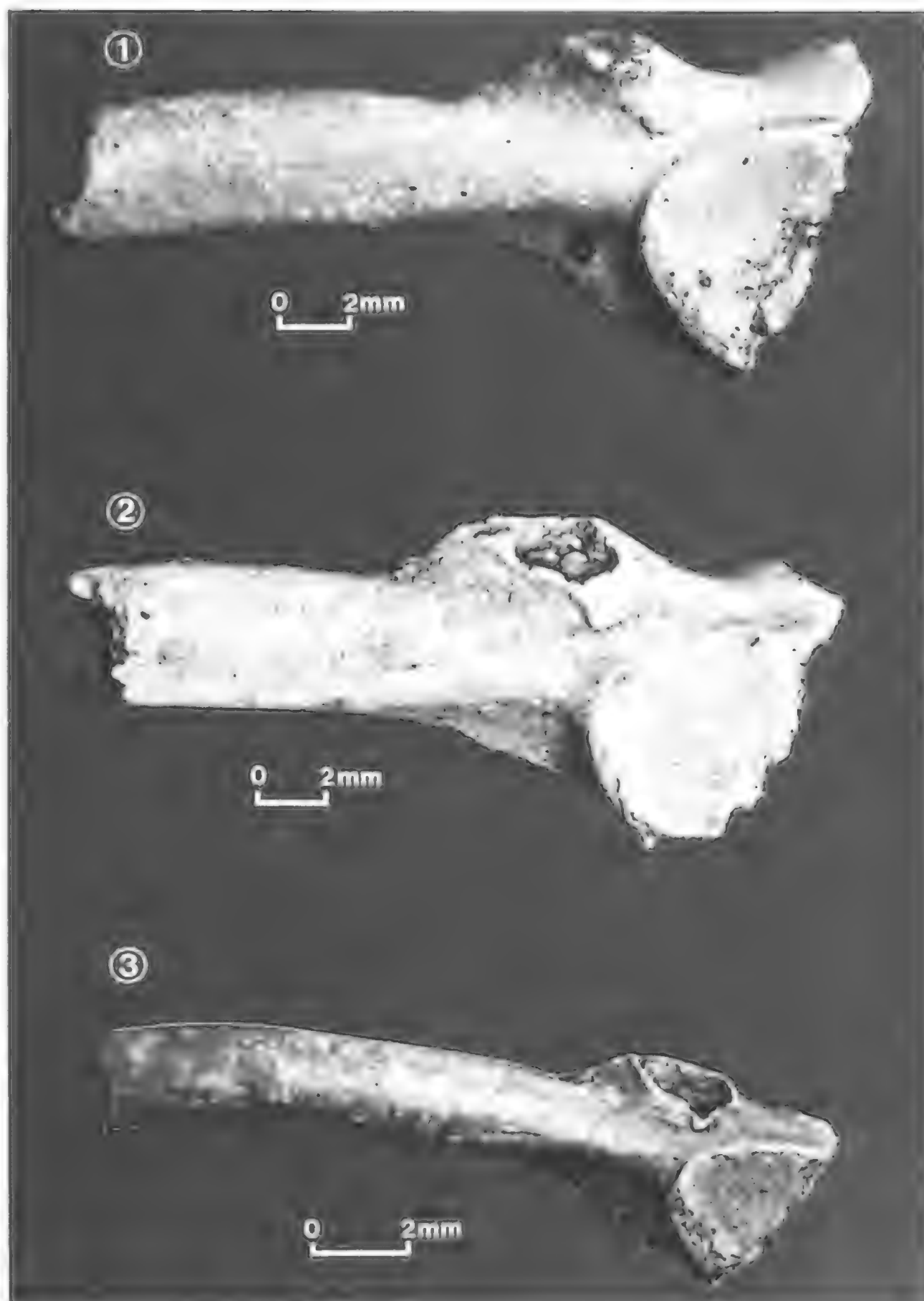
Genus *Cyclorana* Steindachner

The generic features of the pelvis of *Cyclorana* were described by Tyler (1976) based on the examination of the closely related taxa *C. australis* (Gray) and *C. novaehollandiae* Steindachner, and the more divergent *C. dahliei* (Boulenger) and *C. platycephala* (Günther). The only major difference in ilial structure noted amongst these species was the absence in *C. platycephala* of a narrow dorsal rim possessed by the others.

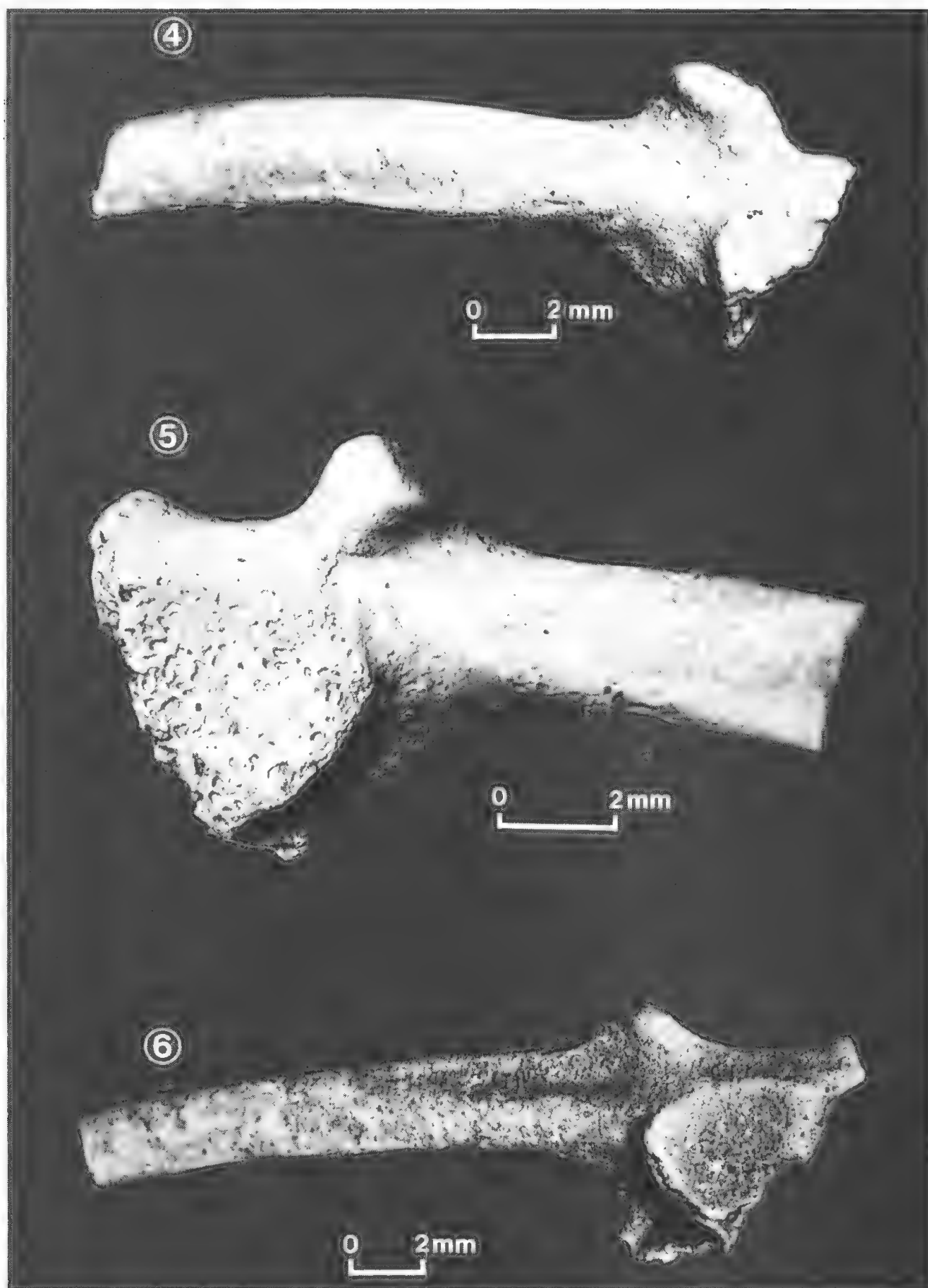
Subsequently *C. dahliei* was transferred from *Cyclorana* to the genus *Litoria* Tschudi by Tyler, Davies & King (1978). For that reason and because of access to all *Cyclorana* species except *C. manya*, it now is possible to redefine the ilial characteristics of *Cyclorana*.

The ilial shaft is long, slender and slightly curved, and in *C. australis* and *C. novaehollandiae* bears a narrow dorsal rim on the lateral surface, and a corresponding depression upon the medial surface. This rim and indentation is lacking in the remaining species. The acetabular rim is narrow and the fossa extensive.

The ventral acetabular expansion is gently rounded and the preacetabular zone is narrow. The dorsal acetabular expansion is well developed and has a gently curved anterior margin. There is a major dichotomy in the form of the dorsal protuberance: inconspicuous and laterally disposed in *C. australis* and *C. novaehollandiae*, but distinctly elevated as a very conspicuous feature in the remaining congeners.



FIGURES 1-3. *Cyclopora cultripes* Parker. 1: QM F 23023; 2: QM F 23024; 3: QM F 23029.



FIGURES 4–6. *Cyclorana* and *Limnodynastes*. 4: *Cyclorana platycephala* (Günther), QM F 23210; 5: *Cyclorana platycephala* (Günther), QM F 23025; 6: *Limnodynastes* sp. cf. *L. tasmaniensis* Günther, QM F 23022.

Cyclorana cultripes Parker

Figs 1–3

Material: QM F 23023, left ilium; F 23024 left ilium; F 23029 left ilium.

The ilial characteristics of *C. cultripes* have not been reported. The fossil material listed above conforms to ilia dissected from extant material principally in the unusual form of the dorsal prominence on the ilial shaft which is elongate, and extends medially over much of its length. As indicated in Figs 1–3 the dorsal prominence has a length equivalent to the diameter of the ilial portion of the acetabular fossa. In each of the fossils the lateral extremity of the dorsal prominence has been abraded.

Cyclorana platycephala (Günther)

Figs 4–5

Material: QM F 23210, left ilium; F 23025 right ilium.

In its overall habitus *C. platycephala* is the most divergent of all of the members of this genus. What sets it apart is the large flat head with small eyes protruding from the dorsal surface, and the extensively (usually fully) webbed toes. The ilium is equally distinctive by virtue of the highly developed dorsal prominence, which rises high above the ilial shaft in an almost cylindrical form.

Family LEPTODACTYLIDAE

Sub-family LIMNODYNASTINAE

Genus *Limnodynastes* Fitzinger*Limnodynastes* sp. cf. *L. tasmaniensis* Günther

Fig. 6

Material: QM F 23022, left ilium.

Amongst the members of the genus *Limnodynastes* the features that are unique to this species are the protuberant nature of the sub-acetabular zone, the lateral groove upon the ilial shaft, and the anteriorly inclined dorsal prominence and dorsal protuberance. These features are shared by modern representatives of *Limnodynastes tasmaniensis*, and particularly specimens reported from Oligo-Miocene sites at Riversleigh Station in northwest Queensland

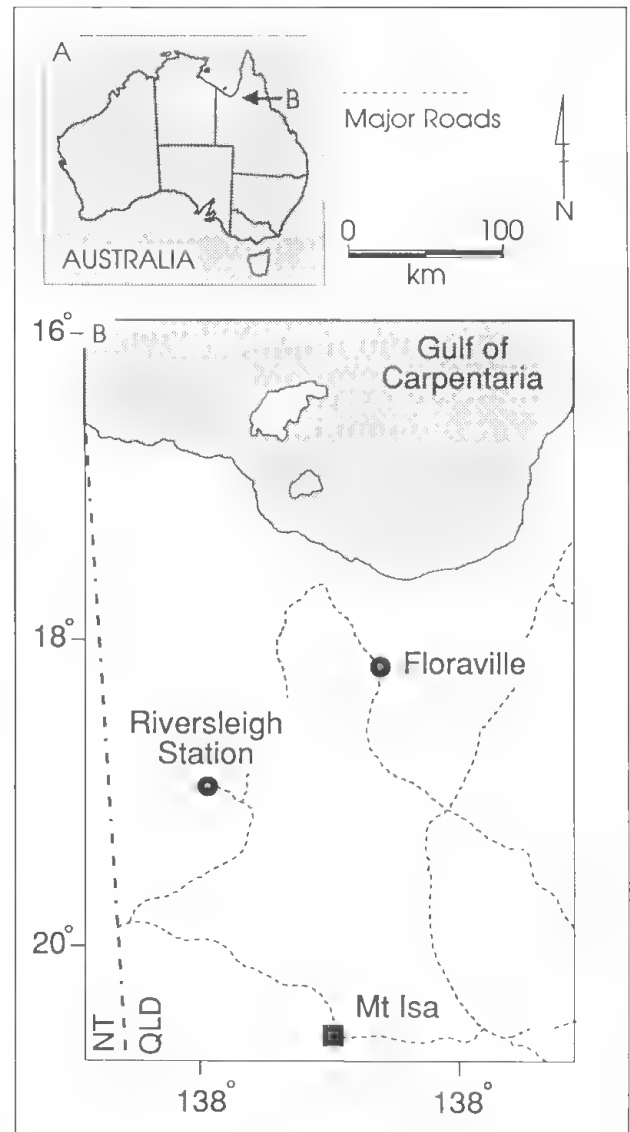


FIGURE 7. Location of Floraville Station and Riversleigh Station, Queensland.

(Tyler, 1990a). The location of Floraville and Riversleigh Stations is shown in Fig. 7.

DISCUSSION

This small assemblage of frogs from the Tertiary of northwest Queensland is significant for several reasons. Firstly because of the presence of two extant species of *Cyclorana*, being the first fossil record of this genus. Neither species has been reported as far northeast. In the case of *C. platycephala* every voucher specimen known throughout Australia until January 1990 was plotted by Tyler (1990b). Floraville Station is just beyond its known modern geographic range. The presence of *C. cultripes* at Floraville Station

similarly has not been recorded, but it is common at similar latitudes and may be assumed possibly to exist there today; there has been minimal collecting activity in the area.

The presence of *Limnodynastes* sp. cf. *L. tasmaniensis* in this collection is intriguing. The modern species has an extensive distribution throughout eastern and southeastern Australia, and was introduced to Kununurra in the Kimberley Division of northern Western Australia (Martin & Tyler 1978). More recently a second isolated population has been located at Newry Station in the Northern Territory (Tyler, Watson, & Davies, 1983). The interpretation of the presence of the species so far from its known geographic range is that it was introduced there. The location of comparable material at mid-Miocene sites at Riversleigh Station in northwest Queensland (Tyler 1990a), and its presence at Floraville Station in the Plio-Pleistocene collectively suggest a far longer duration of existence in northern Australia of an ancestral form resembling the

modern. Clearly it is possible that the extant Kununurra (WA) and Newry Station (NT) populations should be explored as possible relics, rather than recent introductions.

The mammal fauna at the site is dominated by several taxa of as yet undescribed rodents. There is also a high diversity of marsupials, with some extant genera. The sediments are undated but are suggested to be Plio-Pleistocene by Archer (1982, 1984).

ACKNOWLEDGMENTS

We are grateful to Mr and Mrs Camp for permission for M. A. to work on Floraville Station. The field work was supported by R. E. Lemley, the Queensland Museum and the Australian Research Grants Committee. Comparative studies were aided by S. Bryars and supported by the Australian Research Council. The S.E.M. photographs were prepared by Stuart Mclure of the CSIRO Division of Soils, Adelaide.

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FORM AND FUNCTION IN SCALES OF LIGULALEPSIS TOOMBSI SCHULTZE, A PALAEONISCOID FROM THE EARLY DEVONIAN OF AUSTRALIA

CAROLE BURROW

Summary

A variety of isolated scales and lepidotrichia from the Early Devonian of New South Wales is referred to the palaeoniscoid *Ligulalepis toombsi* Schultze 1968, to date known only by isolated scales. Scales of various forms are attributed to specific regions of the body, on the basis of comparisons with articulated Palaeozoic palaeoniscoids. Mobility of scales in the forward flank region appears to have been constrained by a prominent process projecting from the rostradorsal corner, in addition to the peg, socket and keel of typical palaeoniscoid scales. Such complex interlocking of the scales implies that the body of *Ligulalepis toombsi* was relatively inflexible. Some suggestions are offered regarding the possible mode of locomotion.

FORM AND FUNCTION IN SCALES OF *LIGULALEPIS TOOMBSI* SCHULTZE, A PALAEONISCOID FROM THE EARLY DEVONIAN OF AUSTRALIA

CAROLE BURROW

BURROW, C. 1994. Form and function in scales of *Ligulalepis toombsi* Schultze, a palaeoniscoid from the early Devonian of Australia. *Rec. S. Aust. Mus.* 27(2): 175–185.

A variety of isolated scales and lepidotrichia from the Early Devonian of New South Wales is referred to the palaeoniscoid *Ligulalepis toombsi* Schultze 1968, to date known only by isolated scales. Scales of various forms are attributed to specific regions of the body, on the basis of comparisons with articulated Palaeozoic palaeoniscoids. Mobility of scales in the forward flank region appears to have been constrained by a prominent process projecting from the rostro-dorsal corner, in addition to the peg, socket and keel of typical palaeoniscoid scales. Such complex interlocking of the scales implies that the body of *Ligulalepis toombsi* was relatively inflexible. Some suggestions are offered regarding the possible mode of locomotion.

This is a contribution to IGCP 328: Palaeozoic Microvertebrates.

Carole Burrow, Department of Zoology, University of Queensland, St Lucia 4072 Australia.
Manuscript received 21 April 1993.

Ligulalepis toombsi Schultze 1968 is the only palaeoniscoid so far described from Australian sediments older than the Late Devonian. Although no whole, or even partially articulated, specimens have yet been discovered, *Ligulalepis* scales are distinctive and widespread in microvertebrate assemblages from marine Lower Devonian deposits from south eastern, and possibly western, Australia.

Scales of *Ligulalepis toombsi* were first described by Schultze (1968) from the lower part of the Murrumbidgee Group of Taemas, NSW, in greatest abundance from the *Spinella yassensis* Limestone Member of early Emsian age (probable conodont zone *dehiscens* or *gronbergi* – Campbell and Barwick 1988, Talent 1989). *Ligulalepis toombsi* scales were also reported by Giffin (1980) in a diverse microvertebrate assemblage from the Receptaculites Limestone, a lithic unit some 270 to 400 metres above the *Spinella yassensis* Limestone, and dated as mid-Emsian (probable conodont zone *inversus-laticostatus*). In their checklist of Australian fossil fish, Long and Turner (1984) listed other Australian occurrences of *Ligulalepis toombsi* (see Fig. 1a): the Broken River Group, Queensland, Early Devonian sites in New South Wales, and the Thangoo Calcarene of the Canning Basin, Western Australia (a single scale, identified as cf. *Ligulalepis*, Turner *et al.*, 1981). Scales of a second species, *L. yunnanensis* Wang and Dong 1989, have been reported from the Late Silurian of China. Wang and Dong, in their description of this species (1989: 203), state

that the scale peg, socket, and ligula are absent. Schultze (1968) includes these three features in his generic diagnosis, and so the affinities of *L. yunnanensis* are open to question.

In Schultze's description of *L. toombsi*, the species is not allocated to a family but is left in the 'bucket' grouping, the palaeonisciforms. There is currently no satisfactory classification of the palaeonisciforms (Schultze & Bardack 1987), and the terms palaeonisciform, palaeoniscoid and palaeoniscid are often used interchangeably. Even within the family Palaeoniscidae, genera that are included by some workers have been placed in entirely different families and even different orders by other workers. The term 'palaeoniscid' can be particularly confusing: it is sometimes used in referring to members of the family Palaeoniscidae (e.g. Esin 1990), or of the order Palaeoniscida (e.g. Moy-Thomas & Miles 1971), or of the superorder Palaeonisci and the order Palaeoniscidae (Kazentseva 1964). In this paper, the term 'palaeoniscoid' refers to fishes of the order Palaeoniscida exclusive of the deep-bodied platysomoids. As it is so difficult to categorise articulated specimens, it is understandable that a genus such as *Ligulalepis*, which is known only from isolated scales, should have been identified no more closely than 'palaeoniscoid'.

This paper describes several new types of *Ligulalepis* scales from the Early Devonian of NSW. *Ligulalepis* scales of various forms may be attributed to particular regions of the body, following the pattern of squamation described by

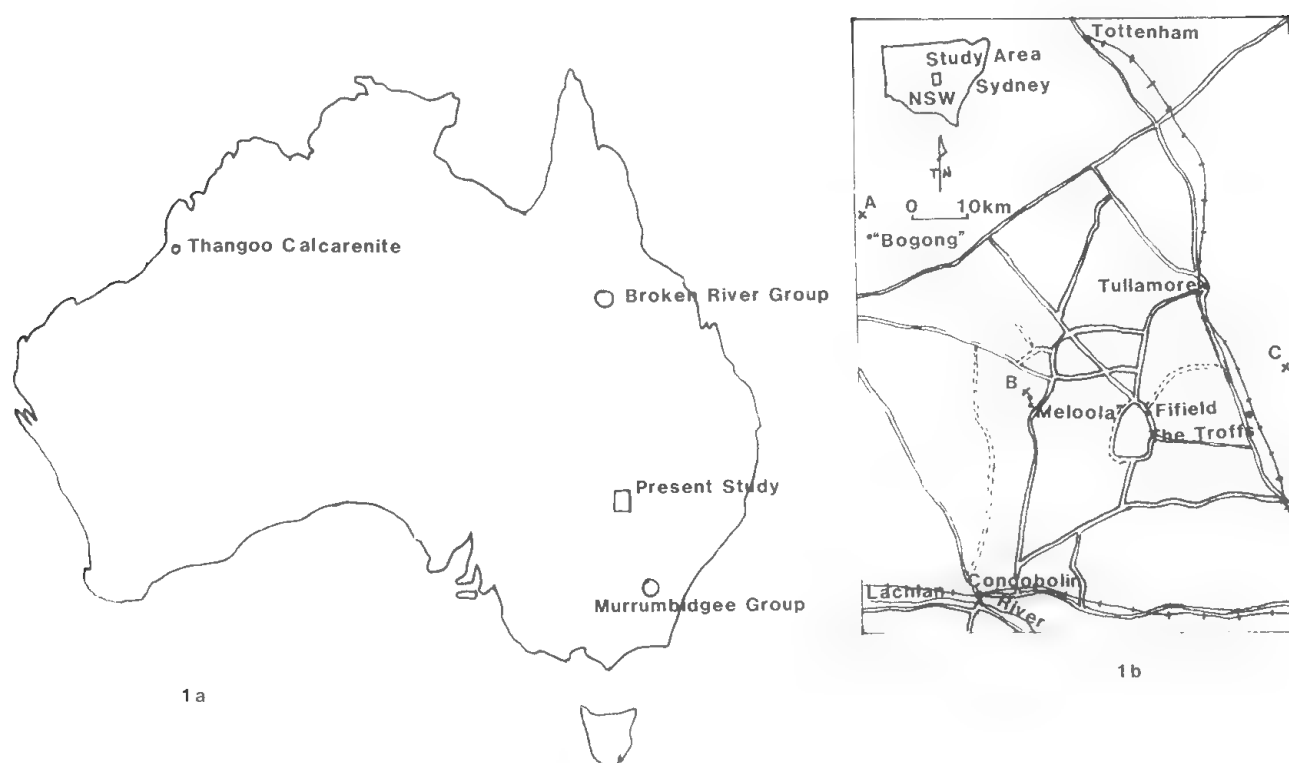


FIGURE 1. a) Map of Australia depicting known sites of *Ligulalepis toombsi* scales. b) Localities of sites with *L. toombsi* scales in study – Locality A: sites C091, C092, C624, C625. B: sites C600, C608. C: site C287. Position of sites based on Australian Topographical Map Series 1:250 000 Narromine and Nymagee. Map adapted from Pickett and McClatchie (1991: Fig.1).

TABLE 1. Distribution of scale types at different sites studied

Sites	T1	T2	T3	T4	T5	T6	T7	T8	T9
Trundle Beds Site C287(7 br + 5 lepidotrichia)	1L 4R	2L	5L 3R	1L	1R	1	1L 1R	1L 2R	0
Mineral Hill Site C625(34 br)	5L 5R	5L 2R	3L 3R	2L 1R	1L 2R	2	1L	1L	0
Mineral Hill Site C092(7 br)	0	0	2R	0	0	0	0	0	0
Mineral Hill Site C624	0	0	0	0	0	0	0	0	1L
Mineral Hill Site C628	0	1R	1L	0	0	0	0	0	0
Mineral Hill Site C091	0	1L	0	0	0	0	0	0	0
Jerula Formation Site C600 – only 2 broken scales									

T=Type, L=Left, R=Right, br=broken.

Esin (1990) in the Permian palaeoniscid *Amblypteria costata* Eichwald.

MMC = Fossil Collection of the Mining and Mineralogy Museum, Sydney.

MATERIAL

The study is based on 67 complete scales which are classifiable into 9 types, 50 pieces of scales, and 5 lepidotrichia. In addition, there are several pieces of dermal bone, bearing the chevron pattern of ornament characteristic of ganoid scales. Scales described in this paper came from residue limestone samples treated with acetic acid by Dr John Pickett (Geological Survey NSW) in searching for conodonts. The parent sites are in the Gleninga Formation of the Mineral Hill Group, Trundle Beds of the Trundle Group, and the Jerula Formation; all being in the Murda Syncline of western NSW, of *pesavis* and/or *sulcatus* conodont zones (Pickett 1992, Pickett & McClatchie 1991; see Fig. 1b). Table 1 details the distribution of scale types for the various localities;

SCALES OF *LIGULALEPIS TOOMBSI*

Schultze (1968) attributed four scale forms to *Ligulalepis toombsi*. Of these, the scale selected as holotype differed from all known palaeoniscoid scales in having its rostro-dorsal corner developed into a prominent tongue-shaped projection (described as 'löffelförmig', or spoon-shaped, by Schultze 1968: 346; see Figs 2,3). In nominating a scale as a holotype, it is conventional and appropriate to choose an example from 'the anterior and middle parts of the lateral surface of the fish body on which the majority of morphological features are distinctly manifested' (Esin 1990: 93). In the case of palaeoniscoids, scales from other areas of the body may be referred to the same species by virtue of qualitative features – the form of the anterior margin of the

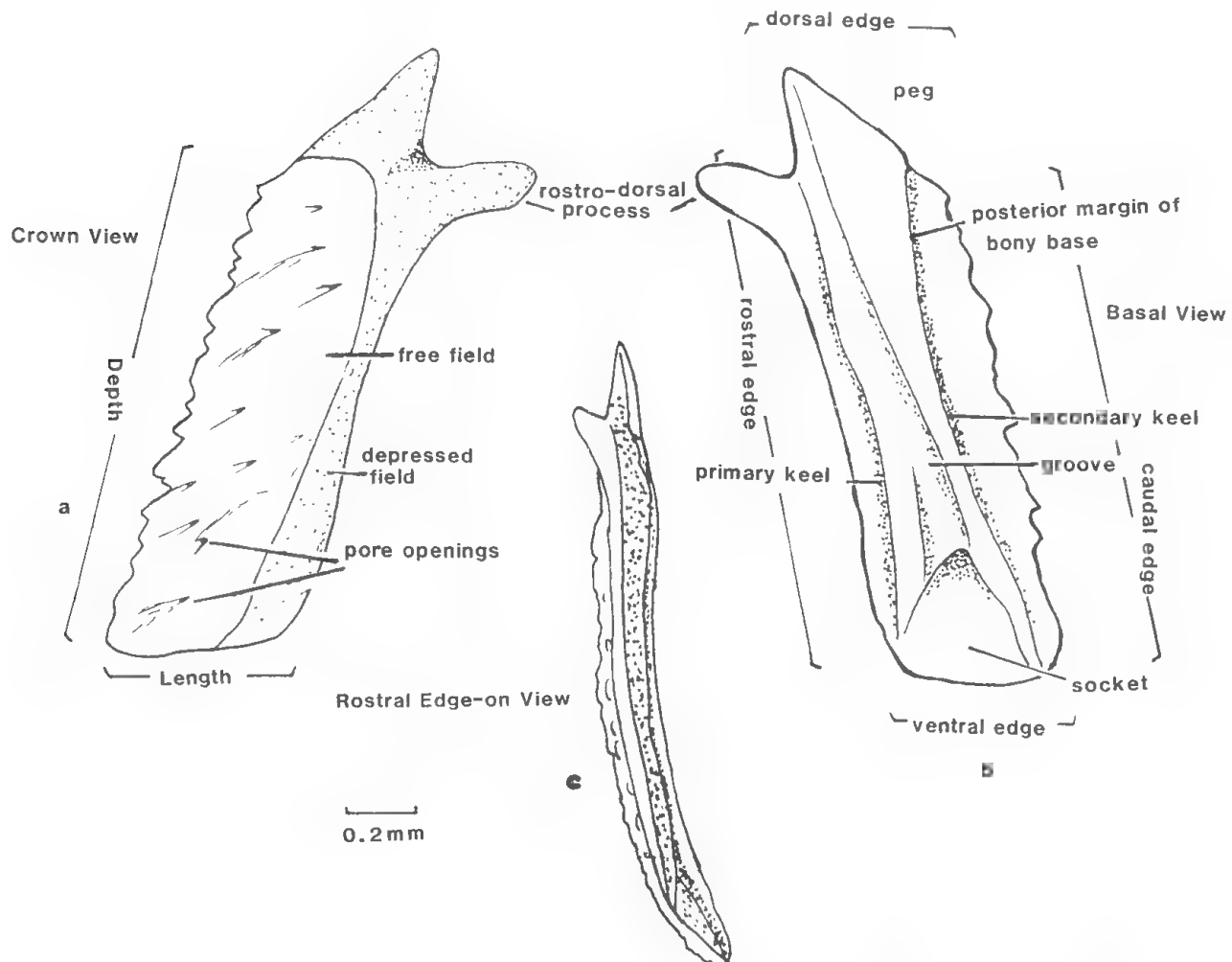


FIGURE 2. *Ligulalepis toombsi* Schultze cf. Holotype scale from area A, with descriptive nomenclature as used in text – a, crown view. b, basal view. c, rostral edge-on view.

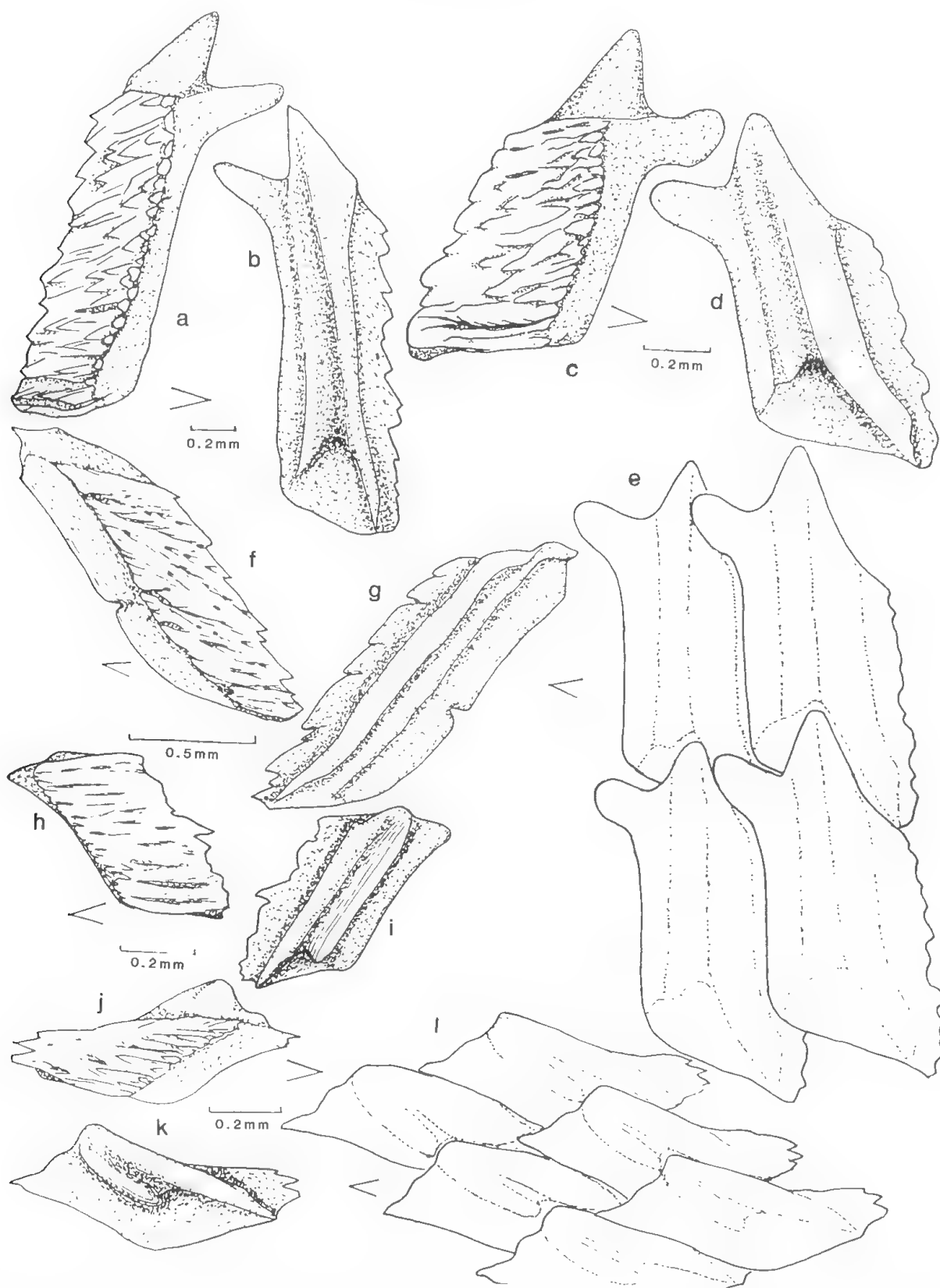


FIGURE 3. *L. toombsi* scales from: The mid-flank region of area A/B: **a**, crown view; **b**, basal view (ref. no. MMMC01926). Area B: **c**, crown view; **d**, basal view; **e**, conjectured basal view of interlocking adjacent scales (ref. no. MMMC01927). Area A, from region immediately behind the shoulder girdle and on the lateral line (note indent on anterior margin of scale): **f**, crown view; **g**, basal view (ref. no. MMMC01928). Area B/C: **h**, crown view; **i**, basal view (ref. no. MMMC01929). Area F: **j**, crown view; **k**, basal view; **l**, basal view of interlocking adjacent scales (ref. no. MMMC01930).

free field, the denticulation of the caudal margin of the scale, and detail of the sculptured ornament. These features were described for *L. toombsi* by Schultze (1968), as follows: anterior margin of the free field has an ornament of small knobs, with main ornament cover extending behind them; posterior margin serrated; numerous pores scattered over the ganoine surface; free field exhibits the chevron pattern typical of ganoine scales.

This study reveals considerable variation in the shape of the rostro-dorsal process, from tongue-shaped to pennant-shaped. Consequently, the term 'spoon-shaped' may be too narrow a description; in this paper it is described merely as the 'rostro-dorsal process'. About 22% of scales possess this process. Scales of *Ligulalepis yunnanensis*, as illustrated by Wang and Dong (1989), appear to lack this process, though this is possibly an effect of breakage (G. Young, pers. comm.).

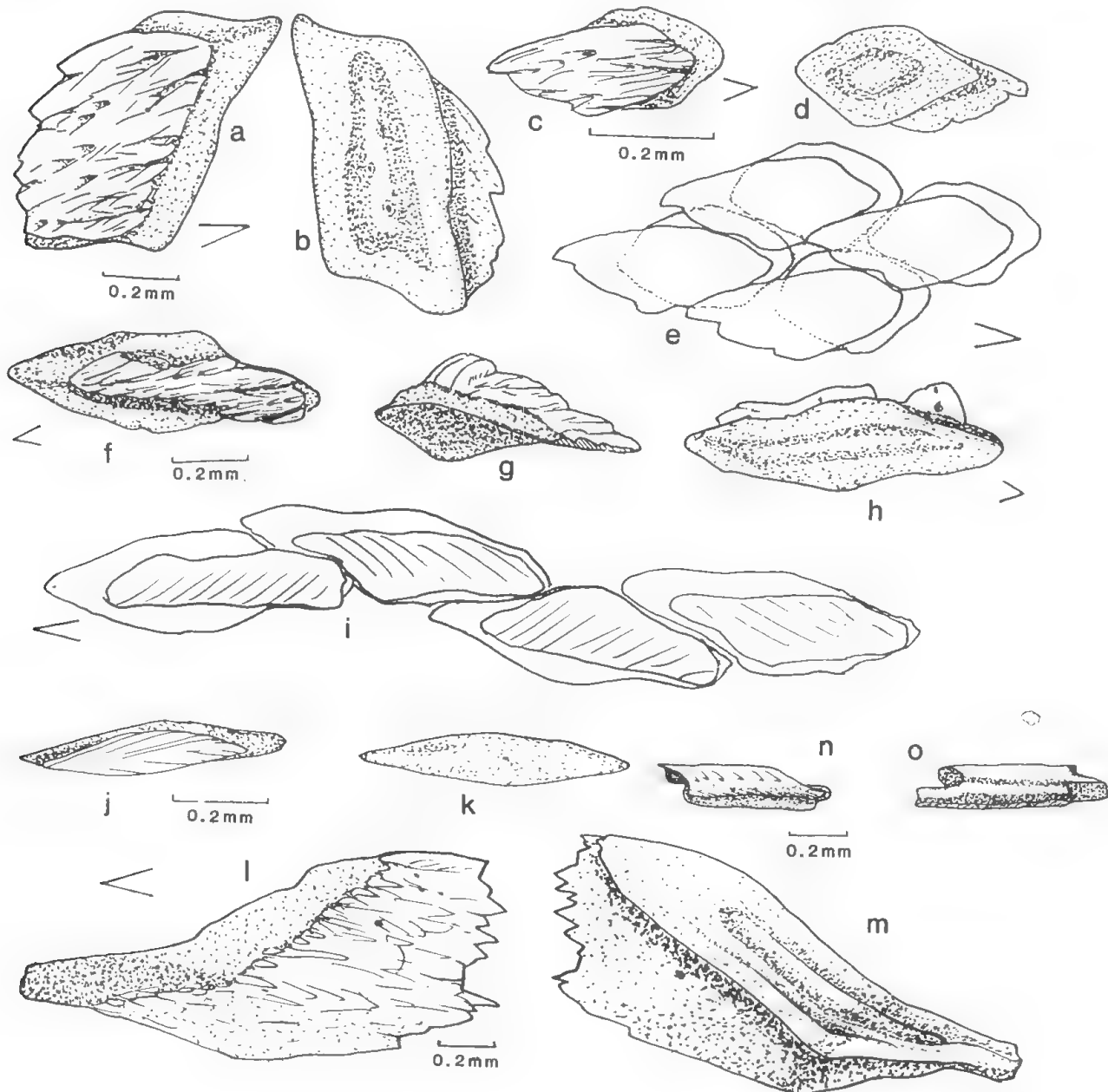


FIGURE 4. *L. toombsi* scales from: Area E: a, crown view; b, basal view (ref. no. MMMC01931). Area G/H: c, crown view; d, basal view; e, basal view of interlocking adjacent scales (ref. no. MMMC01932). Central ridge line – fulcral scale: f, crown view; g, lateral view; h, basal view; i, crown view of adjacent scales (ref. no. MMMC01937). Area D: j, crown view; k, basal view (ref. no. MMMC01933). Area B/F: note dorso-caudal/ventro-rostral orientation – l, crown view; m, basal view (ref. no. MMMC01939). Lepidotrichial scale: n, crown view; o, basal view (ref. no. MMMC01934).



Schultze (1968) stated that the holotype scale is from the anterior half of the body. The height to length ratio of the scales is maximal for each row at the centre of the flank. By analogy with scales on articulated specimens of other Palaeozoic palaeoniscoids (e.g. Gross 1953, Gardiner 1984, Stamberg 1989, Bürgin 1990, Esin 1990), nearly all overlapping scales in this study would have been oriented on the fish's body in rows directed from rostro-dorsal to caudo-ventral, except for scales from the latero-ventral angle.

DESCRIPTIONS

Nine types of scales are attributed to *L. toombsi*, together with lepidotrichia. Descriptive terminology (see Fig. 3) follows Schultze (1968) and Esin (1990).

Type 1 (Figs 3a–e, 5a)

Scales are roughly rhomboidal, with a straight anterior margin except for the rostro-dorsal process. The dorsal peg is high with a pointed apex, matched by a ventral deep triangular socket. Primary and secondary keels are both well developed (as in Fig. 3). The ornamented free-field extends about two-thirds the length of the scale, and overhangs the caudal margin of the scale's bony base. The depth:length ratio varies between approximately 3/1 and 3/2 (excluding peg and flange). Rarely, these scales may have pores for the lateral line canal. Scale ornament resembles that described in the holotype.

Type 2 (Figs 3f, g)

Scales generally similar in shape to those of type 1, but lacking a rostro-dorsal process. The dorsal peg and ventral socket are very weakly developed. Primary and secondary keels are prominent. The length of the unornamented depressed field is about one-third to one-quarter of scale length on the rostral margin, and from one-eighth to one-quarter the depth of the scale, on the dorsal margin. The depth:length ratio varies between approximately 3/1 and 2/1. Scale ornament resembles that of the holotype, though lacking the triangular "knobs" along the rostral margin of the free field.

Type 3 (Figs. 3h,i)

Scales of roughly rhomboidal form, with a straight anterior margin, and a small rostro-dorsal process. The dorsal peg and socket are weakly developed, whereas the primary and secondary keels are pronounced. The length of the unornamented depressed field is negligible, on both the anterior and dorsal margins. The depth:length ratio is about 2/1, and scale ornament resembles that of type 2.

Type 4 (Figs 3j–l, 5b)

Scales of skewed, roughly lozenge-shaped, outline, with an attenuated and sharply pointed rostro-dorsal corner. The peg and socket are present and very broad-based. The keels are parallel to the anterior margin of the scale, which is oriented obliquely (rostro-dorsal to caudo-ventral) relative to the horizontal ornament of the scale. The depressed field is about one-quarter the length of the scale, and the depth:length ratio is about 1/2. Ornament resembles that of the holotype, including the "knobs" along the rostral margin of the free field.

Type 5 (Figs 4a,b, 5c)

Scales of rhomboidal shape, without peg and socket. There are no keels, but the base of the scale has a dark central swelling. The depressed field on the dorsal and rostral margins is about one-quarter to one-fifth the length of the scale. The scales are slightly deeper than long, and their ornament is typical, aside from (like types 2 and 3) lacking the "knobs" along the rostral margin of the free field.

Type 6 (Figs 4c–e, 5d)

Almond-shaped to diamond-shaped scales. Peg, socket and keels are all lacking, but the base of the scale has a dark central swelling. The depressed field extends around the dorsal, rostral and ventral margins. The depth:length ratio is about 2/5. The ornamented surface extends to a point overhanging the caudal edge of the base. Scales lack ornament 'knobs' along the margins of the free field.

Type 7 (Figs 4f–i, 5e)

Scales of sub-rhomboidal form with a

FIGURE 5. *Ligulalepis toombsi* scales – (scale bar = 0.1mm) – a, Broken type 1, with large lateral line pore opening (ref. no. MMMC01938); b, Crown view, type 4 (ref. no. MMMC01930); c, Crown view, type 5 (ref. no. MMMC01935); d, Basal view, type 6 (ref. no. MMMC01932); e, Crown view, type 7 (ref. no. MMMC01937); f, Crown view, type 8 (ref. no. MMMC01934); g, 2 lepidotrichia: basal view (left) and lateral/crown view (right) (ref. no. MMMC01936); h, Fragment of dermal bone, showing chevron pattern.

transversely arched base. Peg, socket and keels are absent, but once again the base has a slight dark swelling located centrally. The depressed field extends along the dorsal, rostral and ventral margins. Ornament resembles that in scales of type 6, but raised at approximately 60° from the base and pointing dorso-caudally.

Type 8 (Figs 4j,k, 5f)

Narrow scales of lenticular outline. There are no pegs, sockets or keels, and the base is of uniform thickness. The depressed field extends from the rostral point dorsally to the caudal point, but is very narrow. The depth:length ratio varies from about 1/3 to 1/6. The ornamented surface is almost smooth, aside from a few shallow striations, and does not form an overhang.

Type 9 (Figs 4l,m)

Scales of 'bent' rhomboidal form, without peg or socket. There is a primary keel and a weak secondary keel. The depressed field is about a third the length of the scale. The depth:length ratio is about 2/1, and the long axis is oriented in a dorso-caudal to rostro-ventral direction. The ornament is typical, though it is noticeably more worn on the ventral half; it extends beyond the caudal margin of the scale base.

Lepidotrichia (Figs 4n,o)

These have a long, narrow 'bread-loaf' shape, with a longitudinal furrow in the middle of each side. There is a central peg and socket on some lepidotrichia, of the full thickness of the scale, and a groove running between these on the base of the scale. The lepidotrichia range in length from about 0.6mm to 1.0mm, and their width is about 0.1mm. The flat upper surface is relatively smooth, though pores are present and the surface is lightly striated. In contrast to the body scales, the ornament may extend onto the peg. The 'unnamed palaeoniscoid scales' illustrated by Giffin (1980, Fig. 11) appear to be examples of lepidotrichia from *L. toombsi*.

DISCUSSION

Scale variation according to body area

Having categorised the scales into these different types, the question now is – from which sections of the body might they have come? Morphology of scales is known to vary in consistent fashion from area to area of the body in articulated specimens of palaeoniscoids (Gross 1953, Gardiner 1984, Long 1988, Esin 1990).

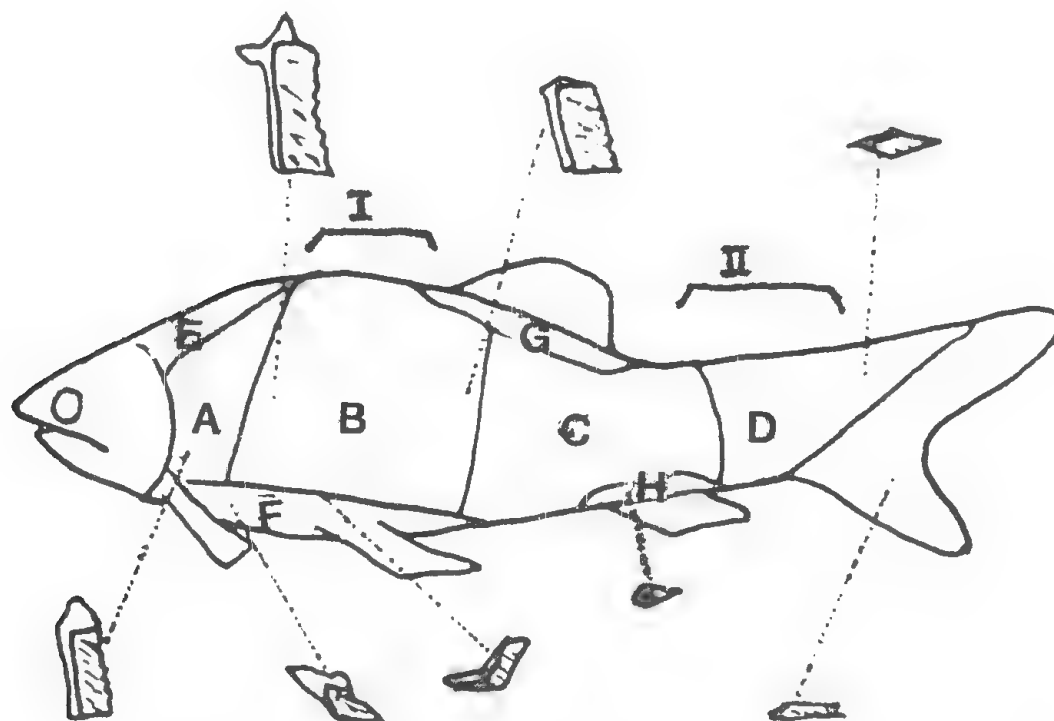


FIGURE 6. Diagrammatic outline of fusiform palaeoniscoid fish, showing distribution of major areas with morphologically distinct scales. a, area behind pectoral girdle; b, front half of flank; c, rear half of flank; d, tail (anterior to fin); e, in front of dorsal fin; f, ventral; g, surrounding base of dorsal fin; h, surrounding base of anal fin I & II, dorsal unpaired scale rows.

Consequently nine types of scales here described for *L. toombsi* may be assigned to specific areas of the body. The following designations are modelled on the scheme of variation described by Esin (1990) for *Amblypterygia costata* Eichwald (see Fig. 6).

There is a decrease in the depth of scales from area A to area D, and from the median line of the fish to its dorsal and ventral margins. Thus the scales with greatest depth/length ratio should be assigned to area A. However, the first row of scales behind the shoulder girdle would not include forms depicted in Fig. 3, with their rostrally directed process, and it is for this reason Schultze (1968) assigned scales of type 2 to the area immediately behind the shoulder girdle. The scales would be expected to be well articulated, being in a relatively inflexible area of the body; scales of type 2 fit the criteria for scales along the rostral margin of area A, overlapping scales of type 1.

Scales of type 1 probably came from areas A and B, overlapping type 3 scales towards the B/C margin.

Scales in area C would not be expected to be highly articulated with each other, as interlocking devices (keels, pegs, sockets and, in the case of *L. toombsi*, rostro-dorsal processes) are weakly developed or absent on scales from more flexible areas of the body (Esin 1990). Scales of type 3 best fit the criteria exhibited by scales of this moderately flexible area in articulated palaeoniscoids.

Scales in the flexible area D lack articulations and are non-imbricating. Scales of type 8 would seem to fit here, becoming more elongated towards the tail fin.

Scales from area E are expected to have a broad low peg, with keels being weakly developed or absent, and a wide depressed field (Esin 1990). Scales of type 5 match these criteria best. Although they lack a peg, they are of a shape intermediate between that of scales of type 2 and type 7.

With regard to area F, the length of the wholly ventral scales of Palaeozoic palaeoniscoids described to date is invariably greater than their height, and they have poorly developed pegs and sockets, with an extended rostro-dorsal corner and a wide rostral depressed field, for secure anchoring in the skin. Scales of type 4 come from this area. Schultze (1968: Plate 1, figs 6a,b) stated that such scales were definitely from the ventral region. Scales of type 9, with a bent shape and worn ornament on the lower half must surely have

come from the flank/ventral angle of the body. These were the only scales to have a rostro-ventral to dorso-caudal orientation, indicating a ventro-lateral scale row directional inversion.

Scales at the base of the fins are expected to be small relative to neighbouring scales, and to show bilateral symmetry (Esin 1990). Scales of type 6 fit these criteria, and by comparison with scales figured in Esin (1990) they most likely came from the base of one of the paired fins (areas G and/or H).

Scales of type 7 are probably ridge or fulcral scales (areas I and II of Esin 1990). Presumably these were aligned in staggered pairs along the 'ridge' line. No bilaterally symmetrical scales have been observed. In other Devonian, and more recent, palaeoniscoids there is wide variation in the distribution of paired and unpaired fulcral scales. Of those species found in Australia, the Late Devonian *Howqualepis rostridens* Long 1988 has unpaired dorsal and ventral fulcral scales on the posterior half of the body; *Mimia toombsi* Gardiner and Bartram 1977 has unpaired fulcral along the whole body dorsally, and ventrally from the pelvic fin to the tail; *Moythomasia duagaringa* Gardiner and Bartram 1977 has unpaired fulcral in front of all unpaired fins except the anal fin (Gardiner 1984). According to Kazantseva (1976) fulcral were initially paired in palaeoniscoids; i.e., in the primitive condition there were no symmetrical fulcral. As *Ligulalepis* is one of the oldest palaeoniscoids found in the fossil record (Late Silurian of China – Wang & Dong 1989), it would be expected to lack symmetrical (i.e. unpaired) fulcral/keel scales.

Although lepidotrichia are rare, they appear to be of a distinctive form. Like the body scales, their structure indicates they were more tightly locked together than those of other fishes.

Functional interpretations

Scales with high depth:length ratios, from the mid-flank region, are quite strongly curved (Fig. 2c). Perhaps this is of significance in relation to the extra interlocking device – i.e., the rostro-dorsal process. The 'abnormal' palaeoniscoid *Cheirolepis* (see Pearson & Westoll 1979, Pearson 1982) has micromeric squamation and also lacks the typical interlocking devices (pegs and sockets) of its contemporaries, the stegotrachelid palaeoniscoids. *Ligulalepis* scales of the same form as the holotype have the highest depth to length ratio reported for any Palaeozoic

palaeoniscoids, and their strong curvature implies a low scale number per scale row, perhaps 10 or fewer. Scales of platysomoids have a high depth:length ratio, but other features of *L. toombsi* scales would preclude them from belonging to a platysomoid (e.g. their strong curvature, and their rostro-dorsal processes). A box-shaped or circular transverse section would be ruled out by the fact that mid-flank scales show the greatest curvature. A fusiform shape is indicated by elimination of these other possible shapes, and by the correlation shown in this paper between the scale types observed for *L. toombsi* with those observed for more recent fusiform fishes.

There is apparently a correlation between the size of scales and the degree of their interlinking. For example, the Cretaceous palaeoniscid *Cteniolepidotrichia* probably comprises two species (Poplin & Su 1992), one having deep scales equipped with pegs and sockets, and the other having smaller squarish scales without pegs or sockets. The body covering of large scales indicates that *Ligulalepis* did not swim in the shark-like fashion envisaged for *Cheirolepis* by Pearson and Westoll (1979). Peg and socket articulations would have constrained dorso-ventral flexibility, while the anterior processes limited the lateral flexibility of the body. The large interlocked scales probably indicate that swimming involved low amplitude undulations. The scale rows would

have acted to brace the sides of the trunk, preventing twisting of the body. Contemporaneous fish with non-micromeric squamation included many placoderms, whose early forms had armour extending onto the trunk so that the front half of the body was stiffened. Gottfried (1991) suggested that this stiffening, for placoderms and deep-scaled fish, also assisted air ventilation by recoil aspiration, as among polypterids. In any case, *Ligulalepis toombsi* appears to have had the least flexible trunk region of any known palaeoniscoids.

It is not possible to infer the likely habitat of *L. toombsi* by analysis of the other microvertebrate remains in the same samples. At some sites, acanthodian and placoderm scales were most abundant, while at other sites thelodont scales predominate. This diversity of faunal associations may indicate that *L. toombsi* had an extensive ecological range, from near shore environments to further out on the continental shelf.

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CAPE HILLSBOROUGH : AN EOCENE – OLIGOCENE VERTEBRATE FOSSIL SITE FROM NORTHEASTERN QUEENSLAND

GREG MCNAMARA

Summary

The Hillsborough Basin is a narrow graben that parallels the modern coast between Prosperine and Mackay, north Queensland. At Cape Hillsborough, just north of Mackay, Hillsborough Basin deposits outcrop. Here a succession of volcanic and volcanoclastic rocks, oil shales and ostracodite named the Cape Hillsborough Beds are well exposed. The Cape Hillsborough Beds are informally subdivided into a dominantly volcanic succession, termed the Cape Hillsborough volcanics, separated by an angular unconformity from an underlying ostracodite and oil shale succession termed the Wedge Island beds.

CAPE HILLSBOROUGH: AN EOCENE – OLIGOCENE VERTEBRATE FOSSIL SITE FROM NORTHEASTERN QUEENSLAND

GREG MCNAMARA

MCNAMARA, G. 1994. Cape Hillsborough: an Eocene – Oligocene vertebrate fossil site from northeastern Queensland. *Rec. S. Aust. Mus.* 27(2): 187–196.

The Hillsborough Basin is a narrow graben that parallels the modern coast between Proserpine and Mackay, north Queensland. At Cape Hillsborough, just north of Mackay, Hillsborough Basin deposits outcrop. Here a succession of volcanic and volcanoclastic rocks, oil shales and ostracodite named the Cape Hillsborough Beds are well exposed. The Cape Hillsborough Beds are informally subdivided into a dominantly volcanic succession, termed the Cape Hillsborough volcanics, separated by an angular unconformity from an underlying ostracodite and oil shale succession termed the Wedge Island beds.

The Wedge Island beds contain vertebrate fossils including ubiquitous teleost bones, turtle (chelid) bones and crocodile scutes.

Palynoflora extracted from Wedge Island beds oil shale indicates a Middle Eocene age based on correlation with the *Nothofagidites asperus* Zone. A mean K/Ar age of 32.5 ± 0.4 Ma on the Cape Hillsborough volcanics provides a minimum Early Oligocene age for the underlying sediments and the Cape Hillsborough fossil fauna. The fauna is therefore derived from one of the better dated Early Tertiary vertebrate fossil sites in Australia.

G. McNamara, Department of Earth Sciences, James Cook University of North Queensland, Townsville 4811. Manuscript received 26 August 1993

Cape Hillsborough is a coastal promontory on the northeastern Queensland coast located between Mackay and Proserpine (Fig. 1). Hillsborough Basin sediments and volcanics are well exposed here. The Hillsborough Basin is a narrow graben structure within Palaeozoic volcanic, plutonic and sedimentary rocks. It trends south-southeast from Proserpine under Repulse Bay and the Hillsborough Channel to near Mackay.

The Cape Hillsborough area was probably a horst relative to other parts of the Hillsborough Basin graben which resulted in a thinner stratigraphic pile developing and a sequence of sediments and volcanics which are not readily correlated with sequences elsewhere in the basin (Slessar 1970).

GEOLOGY

The Cape Hillsborough Beds

At Cape Hillsborough, outcrop is dominated by about 300m of felsic and mafic pyroclastics and lava flows overlying oil shale and limestones collectively termed the Cape Hillsborough Beds. The type locality for the Cape Hillsborough Beds

(Clarke *et al.* 1968) takes in all the north – northeastern cliff exposures from Cape Hillsborough to Andrews Point within the Cape Hillsborough National Park (Fig. 2).

The Cape Hillsborough area encompasses all known exposures of Cape Hillsborough Beds (Slessar 1970). They consist mostly of rhyolitic and basaltic lavas and pyroclastics but comprise a complex interfingering of volcanic and volcanoclastic rocks deposited during a short lived episode of pyroclastic volcanism. Small exposures of underlying sediments occur at low tide revealing approximately 15 m of succession. Slessar (1970) interpreted these sediments as the upper part of a more extensive oil shale sequence with which the volcanics are unconformable.

Remapping has confirmed the volcanics and sediments are not conformable but are divided into two units by an angular unconformity. The sediments below the unconformity are informally termed the Wedge Island beds after the key outcrop at Wedge Island. They encompass other sequences recorded from Donna Bay, Mackay Oil Prospecting Syndicate (MOPS) 4 and MOPS 5 drill holes, GSQ Proserpine 1–2RA drill hole and other outcrops mapped by Slessar (1970) but not relocated by the author (Fig. 2). The overlying volcanics are informally termed the Cape

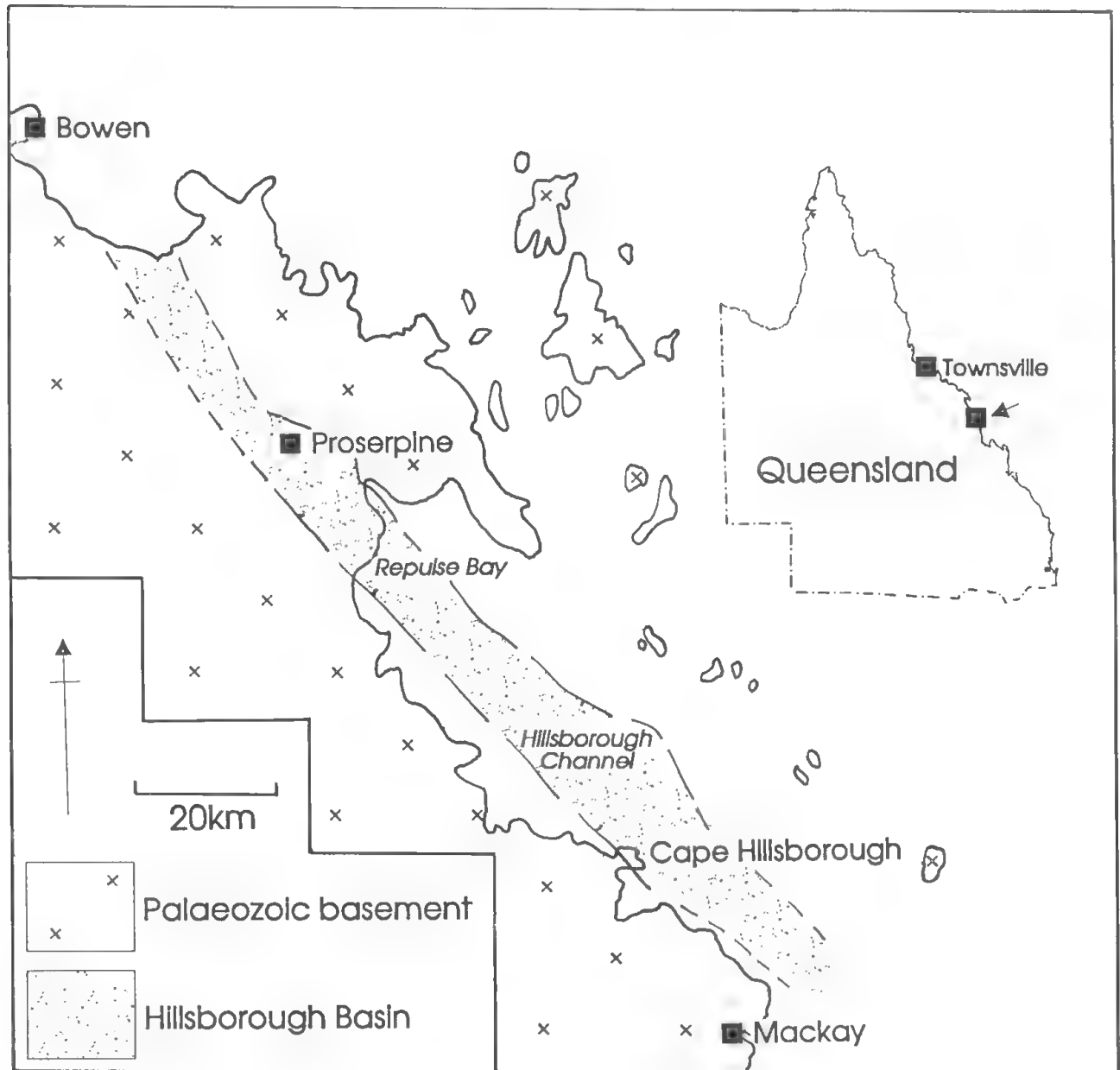


FIGURE 1. Regional geology and location of Cape Hillsborough.

Hillsborough volcanics and include all Tertiary volcanics, volcanoclastics and epiclastics outcropping stratigraphically above the Wedge Island beds in the Cape Hillsborough area (mostly within Cape Hillsborough National Park; Fig. 2).

Slessar (1970) noted the sediments contained fossil plant material, invertebrates and fish bone. Other vertebrate fossils from the Wedge Island beds are described here. Tuffaceous sediments within the Cape Hillsborough volcanics have yielded angiosperm leaves and other plant material (Clarke *et al.* 1968). The existence of fossiliferous tuffs and volcanoclastics in the sequence raises the interesting possibility that vertebrate fossils may also be present within the volcanic pile. The author

located a boulder-sized piece of silicified wood [JCU F12517] in a pyroclastic breccia halfway between Cape Hillsborough and the GSQ Proserpine 1-2RA drill hole (Fig. 2). This indicates significant quiescent periods occurred between eruptive events that would have allowed for the return of vertebrates to the area over the life of the volcanic activity.

Stratigraphic relationships and age of the Wedge Island beds

Slessar (1970) correlated the outcropping Wedge Island beds with the oil shales and

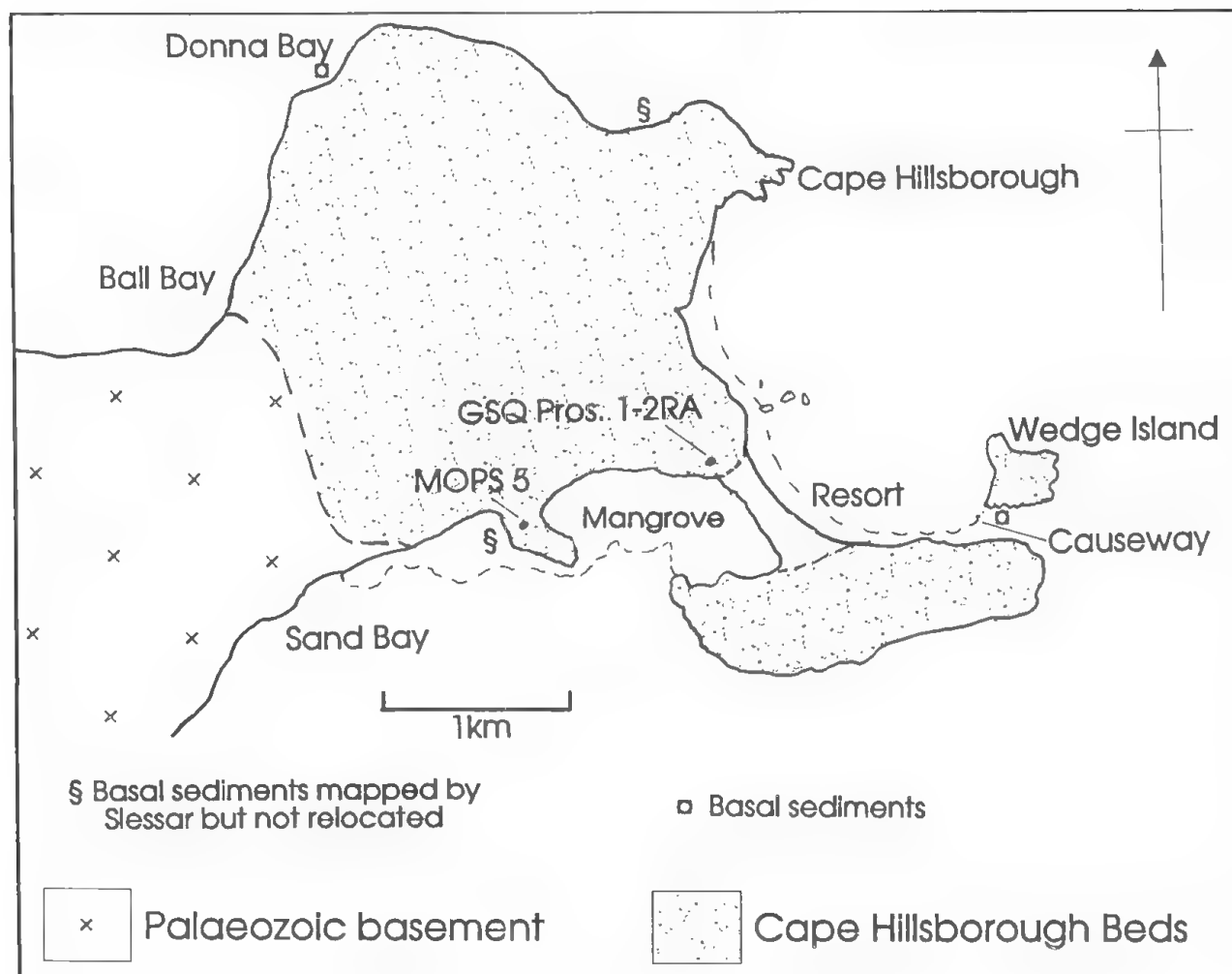


FIGURE 2. Geology of Cape Hillsborough National Park (after Slessar 1970).

sandstones intersected in the wells MOPS 4 and MOPS 5 drilled in 1956. The wells were drilled in the southern part of the Cape Hillsborough study area. The stratigraphic relationship between the sediments and volcanics is not delineated by these drill holes because they only intersected the sediments (Clarke *et al.* 1968). However, there is no doubt Slessar's correlation is correct. The location of MOPS 4 and MOPS 5 is less than 50 m from an (unrelocated) outcrop of the sediments (Fig. 2). Bedding attitudes at this locality and Donna Bay indicate that the sequence dips under the volcanics. There is no evidence of a faulted contact. Intersections recorded for MOPS 4 & MOPS 5 do not include bimodal volcanic units between the sedimentary sequence and the Palaeozoic basement, further confirming the view that the sediments are basal to the volcanics rather than the volcanics being faulted in from below the sediments.

In 1971 a stratigraphic bore (GSQ Proserpine 1-2RA) was put down by the Queensland Mines

Department at Cape Hillsborough (Fig. 2). The Wedge Island beds were intersected approximately 30 m below the volcanics, continuing to a depth of 453 m, thus confirming the interpretation of Slessar. The sediments in this section were logged as interbedded mudstone, shale, siltstone, sandstone and oil shale (Swarbrick 1974).

There is only one outcrop, located at the northern end of the Causeway (Fig. 2), where the contact between the sediments and volcanics is exposed. Slessar (1970) interpreted the contact at the Causeway as an angular unconformity but remapping of the site in 1987 showed it to be a fault. Dip measurements indicate that the Wedge Island beds are folded with the north-dipping limb of a gently plunging anticline truncated against subhorizontal basalt. The exposed fault is steeply dipping and trends almost parallel with the strike of the north-dipping beds (Fig. 3).

Both rock types are brecciated at the contact but no sense of movement is apparent. Assuming the folded sediments are expressing a tectonic event

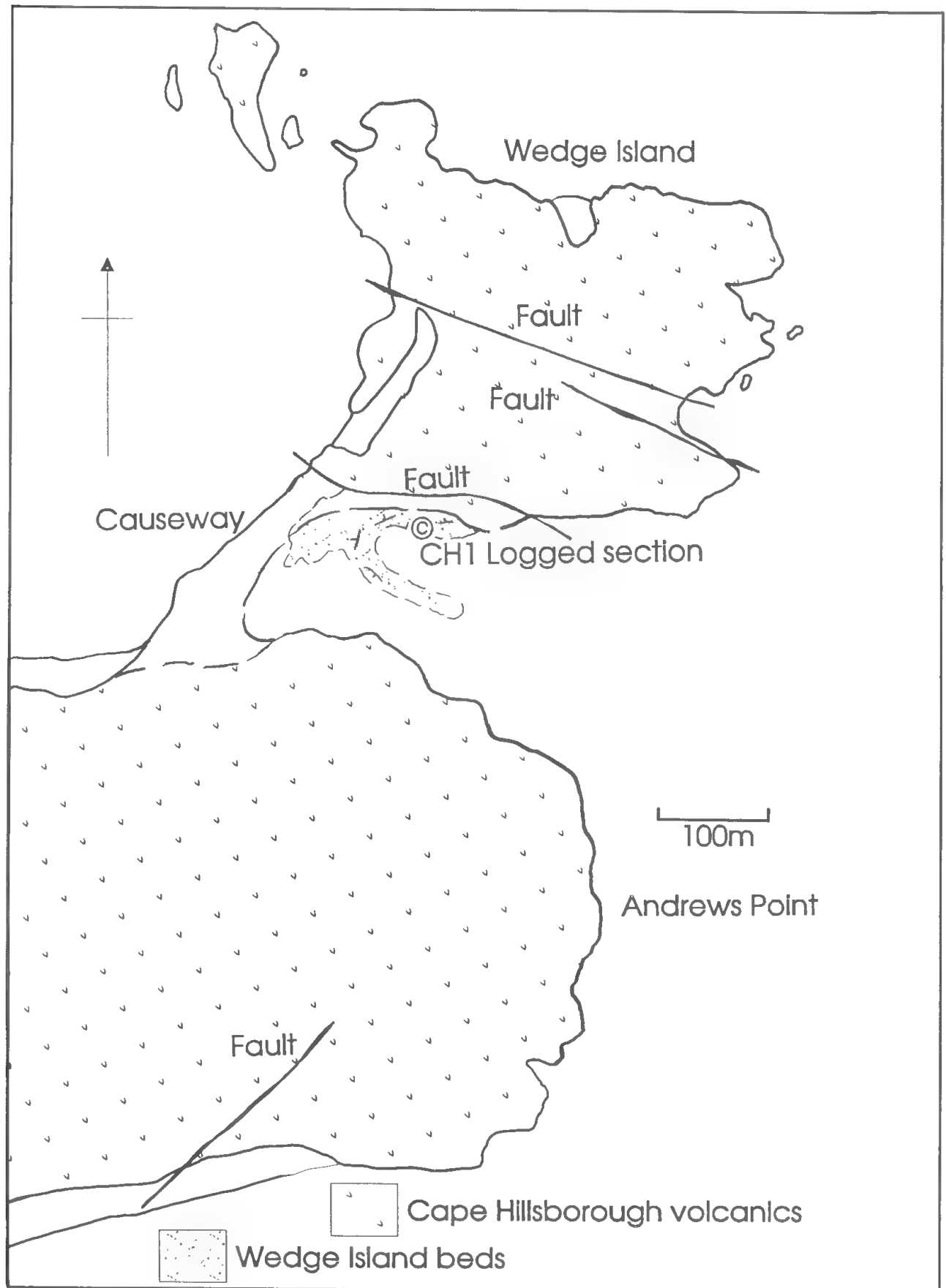


FIGURE 3. The geology of Cape Hillsborough between Andrews Point and Wedge Island and the location of the main fossil deposit at the Causeway.

that pre-dates the volcanism, it follows that the fault block containing them has been uplifted relative to the volcanics. The causeway outcrop sits at a marginally higher elevation than other outcrops of sub-volcanic sediments. It seems unlikely that all other sub-volcanic outcrops would be faulted-in to near the same level. A more likely explanation is that the other outcrops express undisturbed relationships and the causeway sequence, although repositioned by faulting, has not experienced large vertical displacement.

Slessar did not find contacts for any of the other outcrops of Wedge Island beds (Fig. 2) but assumed they were contiguous on the basis of coincident dips and the interpreted angular unconformity at Wedge Island. However, the stratigraphic relationship between the Wedge Island beds and the Cape Hillsborough volcanics is not in question, only the size of the hiatus between them. The timing of tectonism with respect to the volcanism and the stratigraphy revealed in GSQ Proserpine 1-2RA clearly indicate that the Wedge Island beds, and hence the vertebrate fossils they contain, are sub-volcanic. The folding of the Wedge Island beds at the Causeway indicates an angular unconformity *does* exist between the sediments and the Cape Hillsborough volcanics even though the faulted contact does not.

Hodgson (1968) analysed samples from MOPS 4 and MOPS 5 for spores and pollen. MOPS 4 produced a good yield of well preserved pollen whereas MOPS 5 failed to produce a microflora. The palynoflora from MOPS 4 included *Haloragacidites harrisii*, *Nothofagus* cf *N. deminuta* and *Inaperturopollenites* sp. and thus Hodgson (1968) concluded that the sample was probably Lower Tertiary in age. Hekel analysed samples collected by V. Palmieri at Donna Bay and material from MOPS 5. For Donna Bay samples, he recorded elements of the *Cupanieidites orthoteichus* zonule, including its nominate species, indicating a Paleocene to Early Eocene age and probably constrains the maximum age as Late Paleocene (Hekel 1972; Foster 1980). Slessar (1970) listed a flora provided by Hekel for MOPS 5 and noted it contains elements of the *Cupanieidites orthoteichus* zonule together with elements of the *Myrtaceidites eugenioides* and *Gambieriana edwardsii* zonules then believed to be of Paleocene age in South Australia (Harris 1971). Hekel (1972) concluded that the Cape Hillsborough Beds must be Paleocene to Middle Oligocene in age by correlating them with the Hillsborough Basin sediments known at

Proserpine from extensive drilling (eg AEQ Proserpine 1 (Hutton 1980)).

Samples were collected at the Causeway by the author [JCU 36309 – 36320] in an attempt to improve palynological data. The resultant palynofloras were assessed by consultant palynologists McEwan-Mason and Wagstaff, Melbourne and also Neville Alley, South Australian Department of Mines and Energy. The yield of palynomorphs was poor but their preservation was fair to good (N. Alley pers. comm.). The initial assessment (McNamara 1993) indicated a palynoflora that provided no useful biostratigraphic information (N. Alley pers. comm.). Subsequent assessment provided a more useful palynoflora.

The dominant taxa in these samples are *Haloragacidites harrisii* and *Araucariacites australis*. *Malvacipollis diversus*, *Nothofagidites deminutus*, *N. heterus*, *Rhoipites* spp., *Podocarpidites* spp. and *Triorites* cf. *T. orbiculatus* (Foster 1982) are all present in significant numbers.

It is noted that *Proteacidites* frequency and species diversity is relatively low, with the most consistent of the seven species present being *Proteacidites pachypolus*. *Proteacidites kopiensis*, *P. reticulatus*, *Triporopollenites gemmatus*, *Anacolosidites sectus* and *Nothofagidites falcatus* are present. Rare occurrences of *Diporites aspis*, *Crassoretitriteles vanraadshooveni*, *Malvacearumpollis mannanensis*, *Polyodiaceoisporites retirugatus* and *Polypodiidites usmensis* are also noted.

The palynofloras lack the characteristics of Australian Paleocene and Early Eocene assemblages, missing the typical common to locally abundant taxa. The palynofloras are also not typical of Late Eocene and Oligocene assemblages (N. Alley pers. comm.). Significantly, they lack *Triorites magnificus* which is a reliable indicator of early Late Eocene time, its first appearance defining the base of the Middle *Nothofagidites asperus* Zone of the Gippsland Basin (Stover & Partridge 1973) which coincides with the base of Late Eocene.

The first appearance of *Nothofagidites falcatus*, present in the samples, defines the base of the Lower *Nothofagidites asperus* Zone (Stover & Partridge 1973) which corresponds with the early Middle Eocene. This indicates a Middle Eocene age for the Wedge Island beds. A correlation with the *N. asperus* Zone is supported by the lack of *Triorites magnificus* and the presence of *Anacolosidites sectus* which is restricted to the

Lower *N. asperus* Zone. Further support is given by the presence of *Proteacidites kopiensis* and *P. pachypolus* whose range ends in the Lower *N. asperus* Zone (Dudgeon, 1983).

Dudgeon (1983) correlated the central Queensland Yaamba Basin deposits with the *Nothofagidites asperus* Zone using a very similar palynoflora. It too was derived from an oil shale succession. This suggests the Rundle, Yaamba and Condor oil shale successions are penecontemporaneous and all Eocene in age. However, diachronous species ranges between Queensland basins and the Gippsland Basin, 15° to the south, must be considered. Foster (1982) and Dudgeon (1983) concluded that apparent upward range extensions of species in Queensland did not invalidate the use of southern Australian data. This does not diminish the problem of diachronous ranges produced by latitudinal effects on the temporal distribution of flora. Latitudinally controlled zones occur earlier in northern sequences rather than later (N. Alley pers. comm.).

Sluiter (1991) noted that floral differences between Eocene Lake Eyre sediments and southern sites are not great, even though Lake Eyre is 9° further north (about half way between the southern sites and Cape Hillsborough). Sluiter (1991) suggested this lack of difference may be due to a weak equator to pole gradient for this period (Kemp 1978). If Sluiter is correct it may mean there is little latitudinal bias in Eocene species distribution and the Middle Eocene age correlation for the Wedge Island beds is reasonable.

McDougall and Slessar (1972) dated six samples (with concordant results) from the Cape Hillsborough volcanics, with a mean age of 32.5 ± 0.4 m.y. (Early Oligocene). This age is consistent with the stratigraphic relationship between the Cape Hillsborough volcanics and the Wedge Island beds and the angular unconformity between them.

The age of the volcanics is commonly quoted as the age of the whole of the Cape Hillsborough Beds which is misleading. A considerable hiatus, perhaps as much as 12Ma, separates the Wedge Island beds and the Cape Hillsborough volcanics.

The new floral data from Wedge Island concurs with previous palynological assessments of an Early Tertiary age. It refines the age of the beds and is significant for two reasons. Firstly, it indicates the deposit is much older than the Oligocene age of the overlying Cape Hillsborough

volcanics. Secondly, it clearly demonstrates a Middle Eocene age for the vertebrate fossils.

Stratigraphy and sedimentology of the Wedge Island beds

At the Causeway outcrops of Wedge Island beds delineate a small anticline gently plunging towards the northwest. The beds inclined at 20° on the northern limb are exposed at low tide and represent 15m maximum vertical thickness (Figure 3). At Donna Bay the thickness accessible above the low water mark is approximately 2m and the facies associations are distinctly different. Both sequences have abundant bone preserved within the coarser facies.

Four facies are recognised:

Facies 1: Ostracodite. A lime-rich, cream-coloured, sometimes cross-bedded sandstone with occasional pebble sized, well rounded, allochthonous clasts and rip-up clasts. Sand grains are principally ostracod skeletons but terrigenous grains of quartz, feldspar and lithics are present. It is generally carbonate cemented and fossil bones (light brown) are present throughout [JCU 36315, 36316, 36318, 36320 & 36321].

Facies 2: Muddy limestone. Cream-coloured, massive siltstone/mudstone. Induration varies from fully lithified to virtually unlithified dependent on the degree of carbonate cementation [JCU 36314, 36317 & 36319].

Facies 3: Grey-brown shale (oil shale). Finely laminated. Oily efflorescence sometimes apparent. Carbonaceous plant impressions present throughout. Poorly indurated, sea washed sections appear massive [JCU 36309, 36310, 36311, 36312 & 36313].

Facies 4: Brown pebbly sandstone. Variable grain size (very fine-very coarse) both laterally and vertically. Grains dominantly terrigenous but ostracods very abundant. Iron oxide staining common. Fossil bone (jet black) present throughout. Carbonate cement [JCU 36322].

The Causeway facies association

Two distinct facies groupings are present in the Causeway section. The base of the logged section is a monotonous sequence of Facies 3. It is at least 7.5 m thick, extends out beyond the low tide mark, and crops out very poorly (Fig. 4). It contains traces of plant material and has yielded pollen and fungal spores but no bone was found.

The oil shale is replaced up section by a

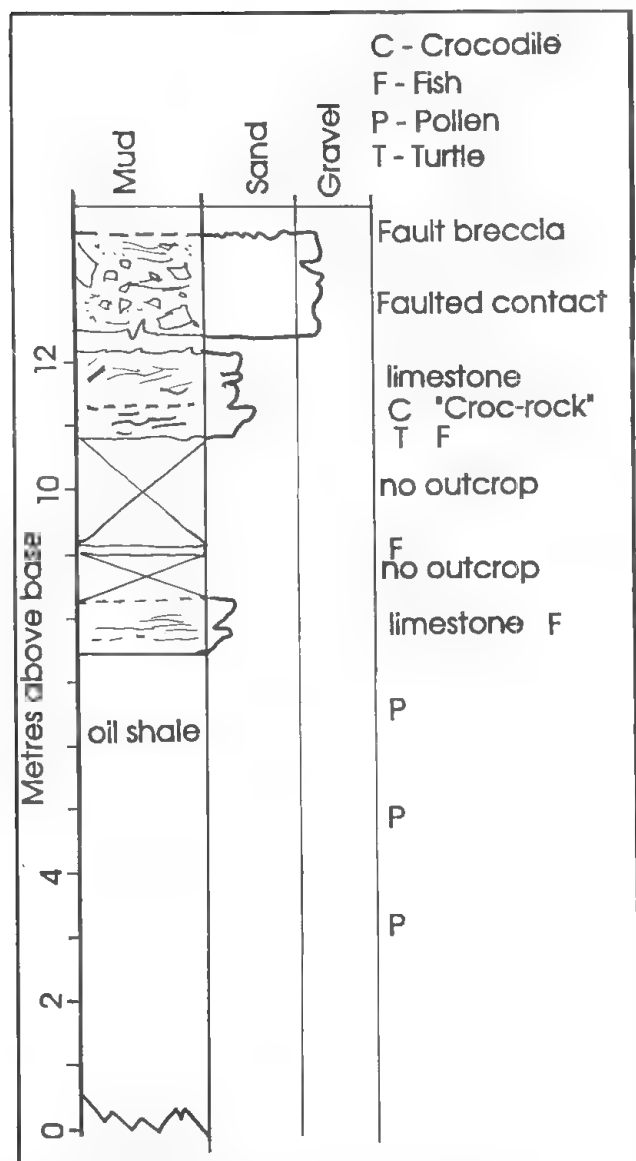


FIGURE 4. Logged section CH1: Wedge Island beds, Wedge Island.

sequence of interbedded muddy limestone and ostracodite but the contact is obscured (Fig. 4). Many of the ostracodite outcrops have sharp bases and appear to grade into the muddy limestone facies. They may represent a fining upwards association but in other outcrops the distinction between the two facies is more pronounced and no fining upwards association is apparent. The maximum thickness expressed by this association is 4.5 m (Fig. 4) but is variable along strike.

The Donna Bay facies association

The thickness available for logging at Donna Bay during low tide amounts to approximately 2m. More is exposed above the intertidal zone but it is mostly covered by a beach boulder bed. Consequently it was decided there was little value

in logging the section. The facies association at this locality does not include either of the Causeway limestone lithologies but the rocks are carbonate rich. Instead there is an interbedded sequence of grey-brown shale and brown pebbly sandstone. The beds of both types grade between each other over a short distance but sharp contacts are uncommon. Carbonate is present as abundant ostracod valves and as cement.

Fossil bone is found in both facies at this locality but principally in the brown pebbly sandstone.

Wedge Island beds environment of deposition

Oil shales develop in anoxic environments such as deep freshwater and hypersaline lakes (Demaision & Moore 1980). Green & Bateman (1981) concluded that the Hillsborough Basin is structurally similar to the East African rift system and that the large anoxic lakes found in that system are a good modern analogue for the depositional environment of the Hillsborough Basin although marine incursions must have also occurred. Green & Bateman (1981) propose a hypothetical 'Condor Lake', at a palaeolatitude of approximately 45° south, developed in an intramontane graben. Sedimentation kept pace with prolonged subsidence, allowing for the accumulation of very thick fluvio-lacustrine sequences of oil shales and other sediments. Dinoflagellates, acritarchs and alginite B in some sections together with anhydrite and gypsum crystals indicate brackish to marine conditions suggesting the basin was sometimes open to the sea (Green & Bateman 1981) whereas the alga *Pediastrum* sp. in other sections indicates a freshwater environment (Foster 1980).

The near-shore environment was dominated by a temperate rainforest flora, similar to forests containing *Nothofagus fusca* type trees found in Tasmania and New Zealand today. Temperatures were probably mild; averaging 17–18°C (Sluiter 1991). The forest was probably relatively closed and probably grew very close to the depositional basin (Martin 1978). This type of temperate forest is ideal habitat for a wide range of birds, mammals and other animals today and there is no reason to think that it would have been any less hospitable during the Eocene.

Slessar (1970) identified ostracods from Donna Bay as *Limnocypridae*, *Bisulcocypris* and *Metacypris* and noted that they indicate a non-marine environment but provided no stratigraphic

insights. Ostracods collected by the author from Wedge Island were too damaged and too well cemented to identify (P. De Deckker pers. comm.). Freshwater ostracods identified from the Rundle and Duaringa oil shale sequences, which are similar to the Wedge Island sequence, suggest deposition in a shallow (approximately 1 m deep) oxygenated lake (Fleming *et al.* 1979).

The ostracodite is not a conventional limestone. It is a fluvio-lacustrine deposit where the dominant grain type is paired ostracod valves [JCU 36321]. Other, non-biogenic, non-carbonate terrestrial grains are common. The bulk of the carbonate in the rock is cement infilling the ostracod valves and occluding pore-space. The valves themselves may have provided some soluble carbonate for precipitation through abrasion and dissolution prior to deposition but they are only calcified chiton, not carbonate. Pebble sized terrigenous clasts and muddy/silty limestone rip-up clasts are well rounded. Cross-bedding is evident in many of the boulders strewn on the causeway but not so obvious in outcrop. Fish bones are entirely disarticulated while the turtle bones are carapace fragments and carapace-plastron sections which do not readily disintegrate, even in energetic streams.

The ostracodite therefore, most likely represents the reworking of fluvial terrigenous input and lacustrine accumulations of ostracod, fish, turtle, crocodile and ?other vertebrate debris. Assuming a freshwater to brackish water environment prevailed, a wave-washed lake margin with numerous small streams debouching into a ?very shallow to shallow lake seems an appropriate environment to generate such a sediment. The ostracodite-muddy limestone facies transitions may even be recording transgressive-regressive lake levels with the anoxic oil shale facies representing the deeper, off shore, sections of the lake. Rip-up clasts may indicate occasional sub-aerial exposure of the marginal lake floor or proximity to a stream flowing into the lake.

The ostracodite-limestone facies is not recorded elsewhere in the Hillsborough Basin (Green & Bateman 1981; Green *et al.* 1984) but is recorded in the oil shale sequences of the Rundle Formation further to the south (Coshell 1983). The Rundle Formation contains sequences of oil shale and ostracodite that are virtually identical to the Wedge Island sequence. Coshell (1983) proposed a shallow lacustrine environment for the deposition of the Rundle Formation sediments and noted that depositional cycles included transgressive and regressive events causing reworking of lake sediments by wave action and

brecciation through sub-aerial exposure. Ostracodite horizons were recognised by Coshell (1983) as representing very shallow lacustrine conditions that only rarely were associated with sub-aerial exposure.

PALAEONTOLOGY

The Wedge Island local fauna

Vertebrate fossils at Wedge Island are confined to the ostracodite and muddy limestone facies. Bone material is commonly an unidentifiable hash but there are abundant spines and vertebrae which clearly indicate that the bulk of this material is from fish.

The Wedge Island local fauna is described below. Unfortunately none of fossils are sufficiently diagnostic to allow the taxon it represents to be identified in detail. The specimens have not been figured for this reason. The concept of the local fauna follows Tedford (1970). Catalogue numbers refer to specimens catalogued and held at James Cook University.

Crustacea

Ostracoda

Ostracod shells form a significant clastic component in the ostracodite facies but can also be found in oil shales and siltstones at Donna Bay [JCU 36323, 36324] (Slessar 1970).

Mollusca

Gastropoda

Casts of naticoid gastropods are common in the Ostracodite and muddy limestone facies at Wedge Island and are very common in some horizons at Donna Bay but cannot be more accurately identified [JCU 36325].

Osteichthyes

Teleostei

Fish spines, vertebrae and other 'fish hash' are ubiquitous and can be found in all of the non-oil shale facies. No articulated material or diagnostic bone has been found [JCU 36326, 36327].

Reptilia

Chelidae

Turtle carapace and plastron sections and

fragments are the most common fossils in the deposit after fish. They probably represent chelid bone but the ornamentation and suturing features are not diagnostic and no further refinement in the identification is possible (Gaffney, pers. comm.; Gaffney 1991) [JCU F12509, F12510, & F12511].

Crocodylidae

Several distinctly crocodilian dermal scutes were found at Wedge Island in an outcrop dubbed 'croc-rock' – CH1: 11 m (Fig. 4). While quite characteristic of the family they are of no help in further identification (Molnar, pers. comm.) [JCU F12512 & F12513].

Problematica

Coprolites were also found in outcrop at croc-rock. While these particular specimens have no diagnostic value they are large enough to have come from a crocodile [JCU F12514]. One specimen however, is reminiscent of stools left by large aquatic birds such as swans [JCU F12515].

Provenance and bias of the Wedge Island local fauna

A shallow lacustrine environment would have provided favourable habitats for many vertebrates but may not have been conducive to the preservation of their remains. Oil shales and other anoxic sediments that preserve plant material are not necessarily suitable for preserving bone. There is very little bone present in the oil shale outcrops at Wedge Island. The casts of fish vertebrae reported by Green and Bateman (1981) indicate bone dissolution is taking place locally within the Condor oil shales.

Conversely, the chemical conditions for bone preservation within the limestones were probably quite good, especially if cementation occurred rapidly after deposition. However the ostracodite was in fact a fluvio-lacustrine deposit involving the transport and reworking of sedimentary components including bones. Such an environment was destructive of articulated remains and of individual bones through mechanical abrasion.

Terrestrial animals would have had their remains abraded during fluvial transport to the lake and through wave action on beach and deltaic bedforms (Napawongse 1981). Aquatic animal remains would also have been subject to wave action but not the dual action of fluvial transport

and lacustrine reworking. Therefore, despite a favourable habitat, the depositional environment of the ostracodite facies mitigated against the preservation of bone of terrestrial origin.

Additionally, biogenic degradation of bone may be expected even before any bone transport begins. Teeth are likely to survive longer than many bones but anything that remains will be greatly diluted in the sediment load relative to the remains of aquatic taxa.

Not surprisingly then, all the bone found to-date derives from aquatic species with the most abundant fossil taxa (fish) simply reflecting the natural aquatic abundance probably present in the depositional system and the number of individual spines, vertebrae and other bones to be found in the average teleost. Turtle carapace bones and crocodile scutes are dense, robust bones likely to survive mechanical abrasion. In addition, turtles and crocodiles are likely to be common taxa in a lacustrine environment and each individual has a large number of such bones or scutes.

RECOMMENDATIONS FOR FUTURE WORK AT CAPE HILLSBOROUGH

It is unlikely that since fish, turtle and crocodiles were present, the lacustrine environment and surrounding terrestrial habitat was hostile to other vertebrates. Even though not a single bone or tooth from a non-aquatic taxon was found, the importance of this site remains undiminished.

Given the small number of Palaeogene vertebrate fossil sites and the degree of age control on the Wedge Island beds, one of the best-dated Early Tertiary vertebrate bearing units in Australia, this unit has good potential for important future discoveries. The potential for vertebrate fossil discoveries in the Cape Hillsborough volcanics should also be explored. It is recommended the succession be routinely prospected.

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THE MIOCENE OSCILLATION IN SOUTHERN AUSTRALIA

BRIAN MCGOWRAN & QIANYU LI

Summary

Warm times are moister times and times of higher sea level. They are represented by more extensive stratigraphic records, richer fossil assemblages, and more precision and confidence in correlation and age determination. The Miocene profile in southern Australia is a profile of episodically advancing seas from the late Oligocene to the early middle Miocene, then a pronounced retreat into the late Miocene. In parallel is the chronological distribution of three warm periods – in the Janjukian stage, the mid-Longfordian stage (early Miocene), and then the twin-peaked Miocene climatic optimum of the Batesfordian-Balcombian stages of the earliest middle-Miocene, 16-15 million years ago. After that, there is a pronounced cooling. That rise and fall at 10^7 years scale is the Miocene oscillation. The planktonic foraminiferal record at lakes Entrance in East Gippsland supports the concept of a rise and fall in sealevel and climate at 10^7 scale with the superimposition of an oscillation at higher frequency – 10^6 years. The match with the global scenario is good. As well, the most pronounced changes in the fossil record are seen within the Miocene climatic optimum, not at the subsequent chilling and fall in sea level. The terrestrial biotas are expected to reveal in due course this three-part Miocene succession : (i) episodically rising trends, Janjukian to late Lonfordian ; (ii) Miocene climaxes, Batesfordian and Balcombian ; (iii) drying and cooling, Bairnsdalian to Mitchellian. The Australian regional stages have a role in the geochronology of Cainozoic biogeohistory ; their boundaries should accord with major natural breaks in the stratigraphic record.

THE MIOCENE OSCILLATION IN SOUTHERN AUSTRALIA

BRIAN MCGOWRAN & QIANYU LI

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Warm times are moister times and times of higher sea level. They are represented by more extensive stratigraphic records, richer fossil assemblages, and more precision and confidence in correlation and age determination. The Miocene marine profile in southern Australia is a profile of episodically advancing seas from the late Oligocene to the early middle Miocene, then a pronounced retreat into the late Miocene. In parallel is the chronological distribution of three warm periods—in the Janjukian stage, the mid-Longfordian stage (early Miocene), and then the twin-peaked Miocene climatic optimum of the Batesfordian-Balcombian stages of the earliest middle Miocene, 16–15 million years ago. After that, there is a pronounced cooling. That rise and fall at 10^7 years scale is the Miocene oscillation. The planktonic foraminiferal record at Lakes Entrance in east Gippsland supports the concept of a rise and fall in sealevel and climate at 10^7 years scale with the superimposition of an oscillation at higher frequency— 10^6 years. The match with the global scenario is good. As well, the most pronounced changes in the fossil record are seen within the Miocene climatic optimum, not at the subsequent chilling and fall in sea level. The terrestrial biotas are expected to reveal in due course this three-part Miocene succession: (i) episodically rising trends, Janjukian to late Longfordian; (ii) Miocene climaxes, Batesfordian and Balcombian; (iii) drying and cooling, Bairnsdalian to Mitchellian. The Australian regional stages have a role in the geochronology of Cainozoic biogeohistory; their boundaries should accord with major natural breaks in the stratigraphic record.

Brian McGowran and Qianyu Li, Department of Geology and Geophysics, The University of Adelaide, South Australia 5005. Manuscript received 2 June 1993.

We have undertaken a research program based on the Neogene foraminiferal succession in southern Australia. As the continent 'drifted' north, subsequent to rapid Australia/Antarctica separation commencing in the middle Eocene, it moved into lower latitudes whilst global climate was deteriorating. Its margin was washed by a series of transgressions. In sharp contrast to the trailing passive margin in the south, the northern margin began, during the Oligocene, to accrete terrains—the latest events in a history of tectonic activity stretching back to the Palaeozoic.

There are essentially three reasons for undertaking this research. One is the relevance of a well-developed, mid-latitude, neritic record of calcareous strata to oceanic drilling to the south of Australia in the Ocean Drilling Program—for the neritic-oceanic interaction bears heavily on the problems of reconstructing a global sea level curve and of clarifying links between palaeo-oceanographic change and palaeoclimatic change. A second stimulus is that the rich neritic record of foraminifera, ostracodes, bryozoa and echinoids, in addition to the molluscs which have long attracted attention, is a splendid resource for studying macroevolution, meaning organic evolution at time scales of 10^6 and 10^7 years. Yet a

third reason is that the terrestrial biotas of ancient Australia have left records susceptible to prolonged argument on the two basic and critical questions: What is the 'age' of the assemblage? What was the 'environment' of its community? By supplying the links between continental landform and biotic evolution on the one hand and global change and its geochronological framework on the other, the marine strata at the continental margins can provide something of a reference for addressing both questions. It is this third reason that preoccupies us here, although it is impossible to isolate it from the others.

CONSILIENCE OF INDUCTION: THE PRIME STRATEGY OF STRATIGRAPHY

The weakest point in virtually all philosophers' systems is the place of history in their scenarios of science and its doing. Among their biological achievements, three luminaries can count some incisive discussion of the fact that not all science is circumscribed by the laws and immanent properties of the physical sciences: Simpson (1963, 1970), Mayr (1982), Gould (1986, 1989).

We can use an example from correlation at

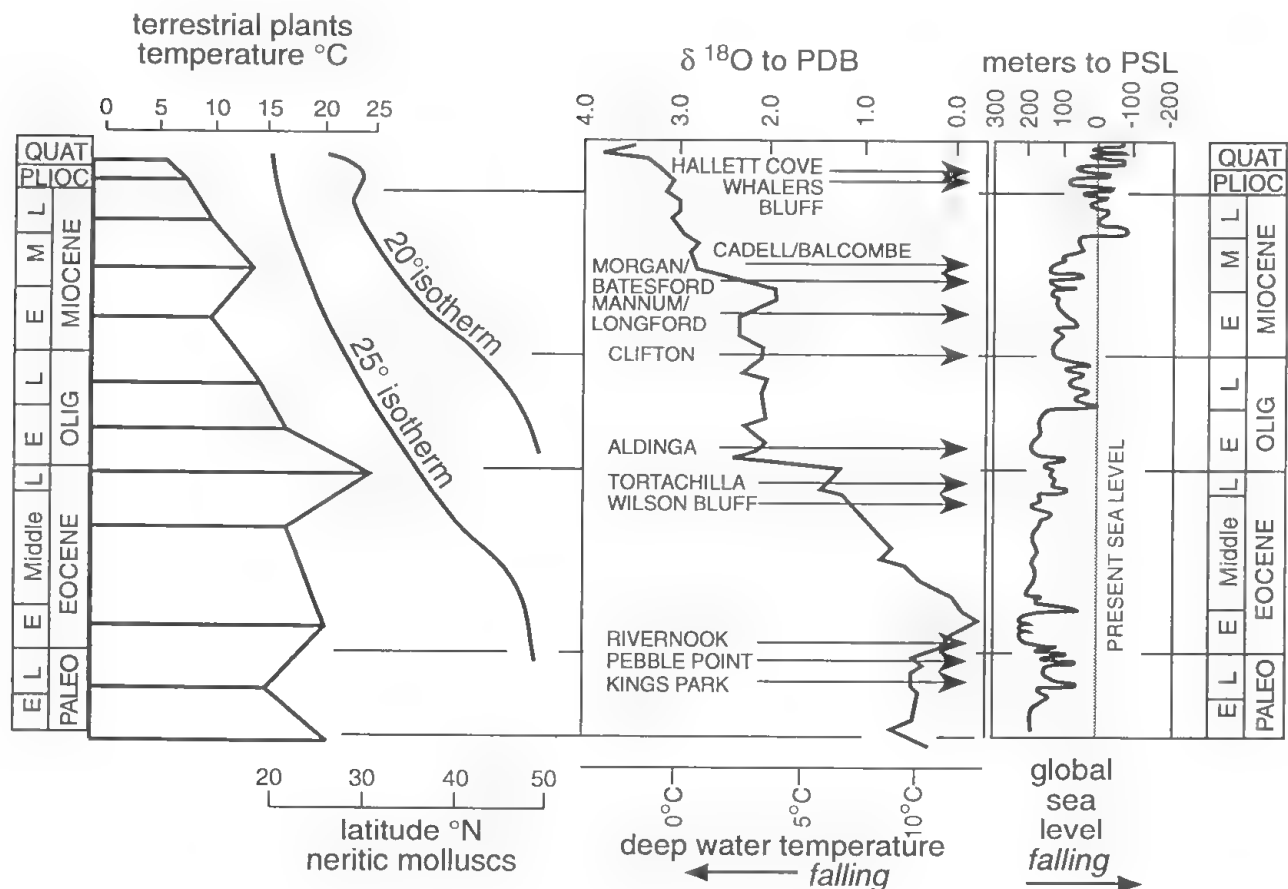


FIGURE 1. Correlation of time series, adapted from McGowran (1991). **Left**, terrestrial plant assemblages from the western U.S.A. yield temperature estimates (Dorf 1955) and molluscan faunas give estimates of latitudinal shift in isotherms (Durham 1950). **Centre**, a composite $\delta^{18}\text{O}$ signal from benthic foraminifera in the deep ocean (Shackleton 1985); the thermometer becomes distorted from the Miocene onward by the ice effect. **Right**, the putative curve of global sea level (Haq *et al.* 1987). Note the close general matches among the various kinds of reconstruction: sea level falls as climate deteriorates through the Cainozoic Era. There are mismatches: the molluscan study missed the Miocene reversal; the major fall in Oligocene sea level lagged behind the spectacular fall in isotopic temperature by the duration of the early Oligocene. Also included are the named incursions and transgressions of southern Australia—benchmarks in the marine record of the southern continental margin.

geological time scale of 10^6 years to make that point. Consider the elegant scenario of Cainozoic change, usually described as global climatic deterioration, in Figure 1 (McGowran 1991). We have long known that the Eocene was a time of global warmth: uniformitarian evidence for that generalization consists of the occurrence of crocodiles, palms, molluscs, corals at higher latitudes than are attained by their modern counterparts (e.g. Lyell 1867). Using the same kind of strategy—extrapolation back from modern biogeographic faunal distribution, including what was known of the environmental requirements of coastal molluscs—Durham (1950) showed that marine isotherms for the western margin of North America have been retreating equatorwards since the Eocene. Similarly, Dorf (1955) could employ terrestrial floras as 'thermometers of the ages' to

give a generalized curve for 40–50°N latitude in the western U.S.A. Both strategies are strong, but both are open to quibbling about the reliability of fossil leaves or of shells as indicators of past climatic states. We add Shackleton's (1985) generalized oceanic bottomwater curve of $\delta^{18}\text{O}$ values from benthic foraminifera. That sort of data too could be and was criticized as susceptible to diagenetic alteration, vital effects, salinity changes in the reservoir—criticisms in the same uniformitarian vein as for the fossil curves, and to be taken seriously. And yet the three curves have a powerful mutual similarity! If quite disparate data from the terrestrial, neritic and pelagic realms of the biosphere show such a good mutual match through geological time, then the chances that we are seeing real climatic changes are suddenly much better than they were for each of the data

sets in isolation. The mutual reinforcement of shells, leaves and isotopes is greater than the sum of the parts. Adding a curve of putative global sea level (Haq *et al.* 1987) to the array, we see a strengthening by further persuasive correlations. Sea level has fallen as temperature has fallen, from the same high point in the early Eocene. (There is a nagging mismatch where the major cooling leads the biggest fall in sea level by the duration of the early Oligocene—also heuristic because it demands explanation.)

That lesson in mutual reinforcement by chronological correlation is at Cainozoic time scales. We can amplify the scenario for the Miocene to make the same point by anticipating a major theme of this paper (Fig. 6). McGowran and Li (1993) have correlated two kinds of curve independently to a revised chronology (W. A. Berggren, pers. comm., 1992). One is the oceanic isotopic evidence for the *Mi* glaciations at 10^6 years' scale, rising then falling on the trend at 10^7 years' scale (Wright *et al.* 1992); and the other is the Exxon sea level curve, also at both 10^7 and 10^6 years' scale (Haq *et al.* 1987). The match at both scales is remarkable, even though the independent correlation to the integrated chronology leaves several mismatches at 10^6 years' scale: coolings should fit sequence boundaries, not maximum flooding surfaces, either because of glacioeustatic lowering of sea level, or because lower sea levels enhance continental-type climates. Thus the mismatches can be targeted for scrutiny and a fine-tuning of the correlations.

In both of these examples it is the chronological correlation of disparate data that counts for most. This strategy has a noble ancestry and yet has been curiously unacknowledged (Gould 1986, 1989). Charles Darwin, 'so keenly aware of both the strengths and limits of history, argued that iterated pattern, based on types of evidence so numerous and so diverse that no other coordinating interpretation could stand—even though any item, taken separately, could not provide conclusive proof—must be the criterion for evolutionary inference' (Gould 1986). As Gould notes, the 19thC philosopher of science William Whewell called this strategy of coordinating different lines of evidence to form a historical pattern, 'consilience of induction'. (No matter that Whewell—coiner of 'uniformitarianism' and 'catastrophism'—was an essentialist philosopher (Mayr 1982) with little grasp of Darwin's iconoclastically historical science; or that he not only rejected the thesis of 'On the origin of species...' but banned the book itself (Gould 1989).)

'Consilience of induction' captures the spirit and the strategy of biostratigraphy. How do the strata and their recorded events fit together as a pattern in space and time, and what does that pattern tell us of biogeohistory? This is not an orderly one-way street from correlation to history, but rather a turbulent two-way, hermeneutic thoroughfare. The mutually reinforcing patterns in Figure 1 show the 'Miocene oscillation' or temporary reversal of the grand Cainozoic trend (McGowran, in Frakes *et al.* 1987) clearly, except for Durham's curves. And that is the simplest reason to reject a view of Australian Cainozoic history entrenched in sedimentology, palaeobotany, geomorphology, neritic palaeontology—that we have a somehow special climatic trajectory brought about by Australia's northwards drift to warmer latitudes. Rejected already (McGowran 1979a; in Frakes *et al.* 1987), that view has been supported again by Zinsmeister (1982) and Darragh (1985). The Australian scenario fits the global pattern too well to need *ad hoc* buttressing by auxiliary hypotheses. (Which is not of course to question the importance of Australia's present position to the modern climate.)

The Oligo-Miocene 'sequence'

Consider Figure 2, drawn in 1977. It is a cartoon, a bold conjecture, of course, which attempts to summarize patterns of strata in space and time, to hammer the message that there is a strong parallelism in time through the full range of sedimentary and tectonic environments. As a first-order generalization the pattern still holds, broadly, although it emphasizes the latest Eocene too much and the latest-middle to earliest-late Eocene too little (McGowran 1989a), and the middle Miocene instead of the early Miocene (see below). Those and other corrections are less important than the remarkable gaps in the early middle Eocene, early Oligocene, and late Miocene, giving four Cainozoic 'sequences'. (There is some fossiliferous sediment of early Oligocene and late Miocene age; these are relative statements.) The gaps consist either of hiatuses well constrained by bounding dates, or of markedly regressive facies not well dated, but assuredly occupying only a small part of the time between good dates, or simply an absence or marked rarity of good biostratigraphic records. The theme is repeated and extended but thoroughly substantiated in the palaeogeographic and facies maps of Australia

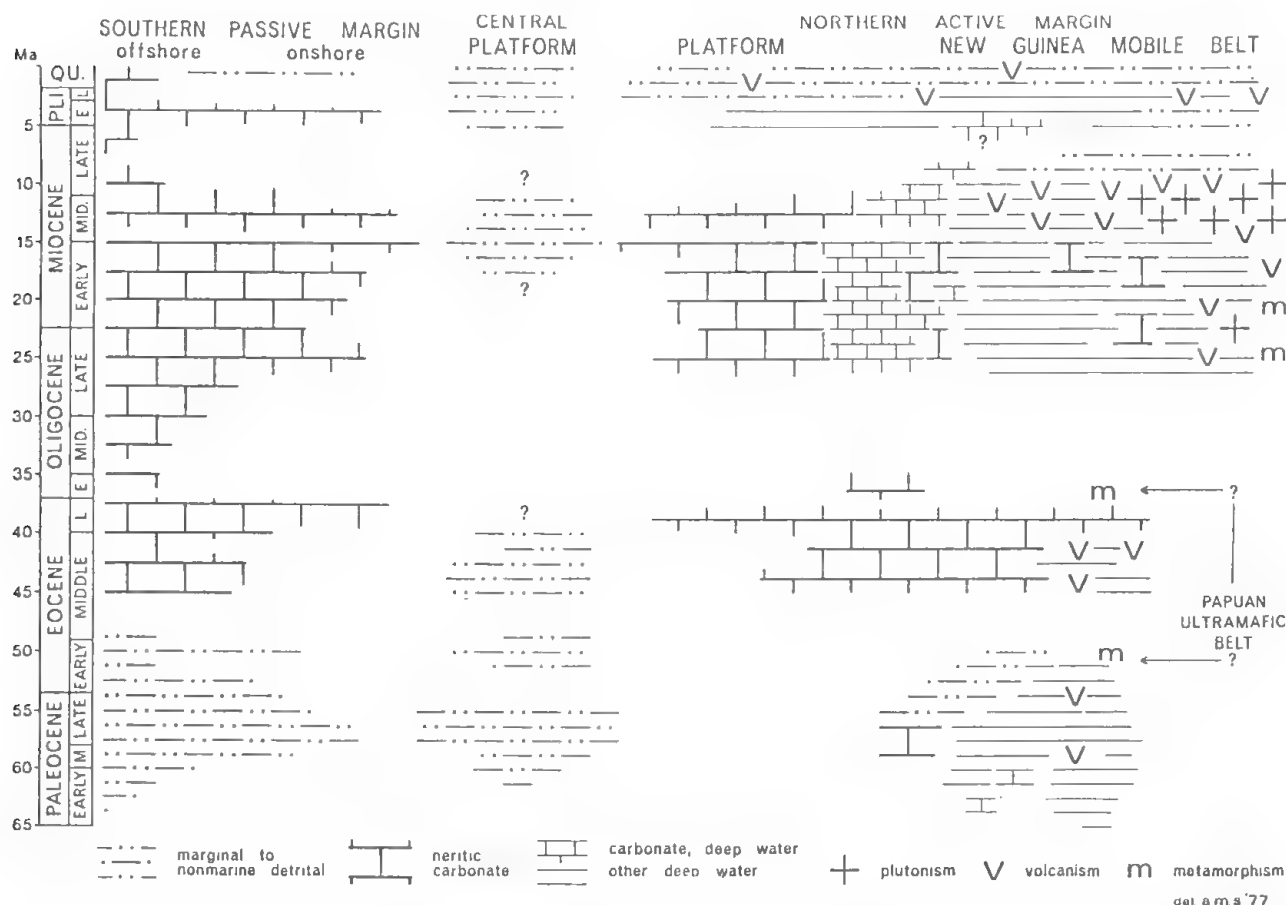


FIGURE 2. Cartoon of sediments versus time across the Australian continent, from McGowran (1979a), intended to show that decades of correlation and age determination—and some interpolation—yielded a pattern of ‘sequences’ bounded by hiatuses. Obviously, much lithological variety and much continent have been omitted. With some adjustment, the broad contrast between a richer early–middle and a poorer middle–late Miocene stratigraphic and fossil record still holds.

(BMR Palaeogeographic Group 1990). Thus their map ‘Cainozoic 2’, 52–37 Ma (actually representing most accurately the 4 Ma time slice across the middle/late Eocene boundary, 42–38 Ma) displays a generous array of marine facies especially on the southern margin, and nonmarine facies in palaeodrainages and major catchments. It is remarkably similar to ‘Cainozoic 4’, 30–10 Ma (actually representing most accurately the time across the early/middle Miocene boundary, 20–15 Ma), and to ‘Cainozoic 6’, 5–2 Ma (Pliocene). In stark contrast are ‘Cainozoic 3’, 37–30 Ma (early Oligocene) and ‘Cainozoic 5’, 10–5 Ma (late Miocene). At those times all facies, marine and nonmarine, at the margins and across the continent, shrink almost to vanishing point. The cartoon in Figure 2 still holds validly as another way of depicting the Miocene ‘sequence’. The sequence is the regional stratigraphic manifestation and signal-bearer of the Miocene oscillation.

Stratigraphic correlation and classification

Australia is antipodeal to the region where Cainozoic stratigraphy developed; it is separated from that region by the tropics; and its terrestrial biotas and much of the neritic biotas carry the stamp of prolonged isolation from the rest of the world. Its northern, heavily vegetated margin in New Guinea excepted, the continent has been stable, lacking the thick, rapidly accumulating sedimentary successions subsequently uplifted and deeply exposed by erosion, as in the Americas and the Himalaya, for example. Instead, we have thinner and more scattered sections with less outcrop and a carapace of deep weathering and duricrusting. Biogeography and the stratal record accordingly give us a double problem: to piece together a highly composite, regional, stratigraphic and biostratigraphic succession; and to correlate that record with the global geochronological standards. As if there were not complaints enough

already, there is a further problem special to the Cainozoic at large, as outlined by Martin Glaessner in a masterful study of half a century ago:

Biostratigraphic correlation of Mesozoic marine deposits is based on zones which are either worldwide or at least useable within the wide limits of a palaeo-zoogeographic province. Correlation of Tertiary deposits is a much more difficult problem on account of climatic differentiation, topographic isolation, and close stratigraphic subdivision of deposits representing a comparatively short time interval. No worldwide scale of fossil-zones based on well-defined ranges of a set of index-species exists. A sequence of Tertiary faunal assemblages was long ago established in Europe and it is not surprising to find that workers in other continents first turned to this sequence for guidance by means of direct comparison and correlation. As long as no scale of zones is available, the next higher unit in stratigraphic classification, the stage, must be the basic unit for measuring geologic time. The recognition of the European stages in the East Indies proved so difficult that a number of workers gave up and even condemned attempts at inter-continental correlations (Glaessner 1943: 52).

In southern Australia the development of correlation and age determination can be divided into two major periods:

(i) Until the 1940s. The biostratigraphy of the marine record was dominated by molluscs, as it was elsewhere (e.g. Singleton 1941; Darragh 1985). Application of the Lyellian method of percentages of extant taxa had little success, also as elsewhere. Local stages were erected, partly in reaction to the ensuing confusion, partly to facilitate progress within the continent while correlations further afield remained contentious or impossible. But the stages were biological in their essence, based as they were on distinctive macrofaunas based on type localities. 'Correlation was by comparison of gross suites of described molluscs' (Darragh 1985). Until Singleton (1941) redefined the stages on lithological criteria, bringing some order into chaos, the stages were losing their value for two reasons—by becoming 'nothing but convenient labels for certain well-known collecting grounds', and by sometimes being impossibly inclusive, sometimes too restricted to be useful (Glaessner 1951). Re-reading Singleton half a century later, one is struck by how little biostratigraphy he includes—fossils there are aplenty, but they are hardly central to the ordering and arranging of the stratigraphic record. And one is startled to be reminded that Singleton lists not one confident identification of

pre-Oligocene strata across the continent, except for the limestones in the northwest where Irene Crespin's studies of larger foraminifera—not molluscs—allowed correlation with the Indo-Pacific letter classification erected in the Netherlands East Indies.

(ii) 1940s to present. Foraminifera were described from the Neogene of southern Australia as long ago as the 1880s (Howchin, 1889) and the same author is acknowledged as one of the very first workers anywhere to describe them from a borehole (Howchin, 1891). Even so, the first substantial shift away from the molluscs and towards the more extensive use of foraminifera and lithostratigraphy in the definition and characterization of stages was delayed for decades, until Crespin (1943). But the most noteworthy event in retrospect was the crisp presentation of three zones and their significance by Glaessner (1951). The *Hantkenina alabamensis*, *Victoriella plecte*, and *Austrotrillina howchini* Zones were non-contiguous—upper Eocene, upper Oligocene, lower Miocene respectively—which upset some purists, but they surely succeeded in fulfilling Glaessner's aim of providing a framework for the future clarifying of the problems seething in the morass of correlation and nomenclature in the southern Australian Tertiaries. As Tertiary correlations and age determinations progressed, most rapidly where microplankton could be used, they did so without the benefit of local stages (e.g. Glaessner and Wade 1958; Wade 1964; Ludbrook 1971), or with the stages merely appended to the biostratigraphy (e.g. Carter, 1964; Ludbrook and Lindsay 1969). Indeed, Singleton (1968) became sufficiently sanguine about progress in clarifying foraminiferal and macrofaunal biostratigraphy to abandon the local stages altogether. McGowran, Lindsay and Harris (1971), attempting the first comprehensive correlation of the local stages to a modern 'global' geochronology, were not at all sure that we were as advanced as all that, and felt that we still needed a local chronostratigraphic focus for the diverse biostratigraphic evidence coming from continental to open marine environments. Even so, one of the authors (Lindsay 1981, 1985) subsequently used the stages extensively whereas another (McGowran 1978-1988) did not. By and large, local stages have not prospered as essential chronostratigraphic tools in this region. In the most comprehensive modern surveys of the classical Tertiary marine fossils, the molluscs, the local stages are used but they do not loom very large (Ludbrook 1973, Darragh 1985).

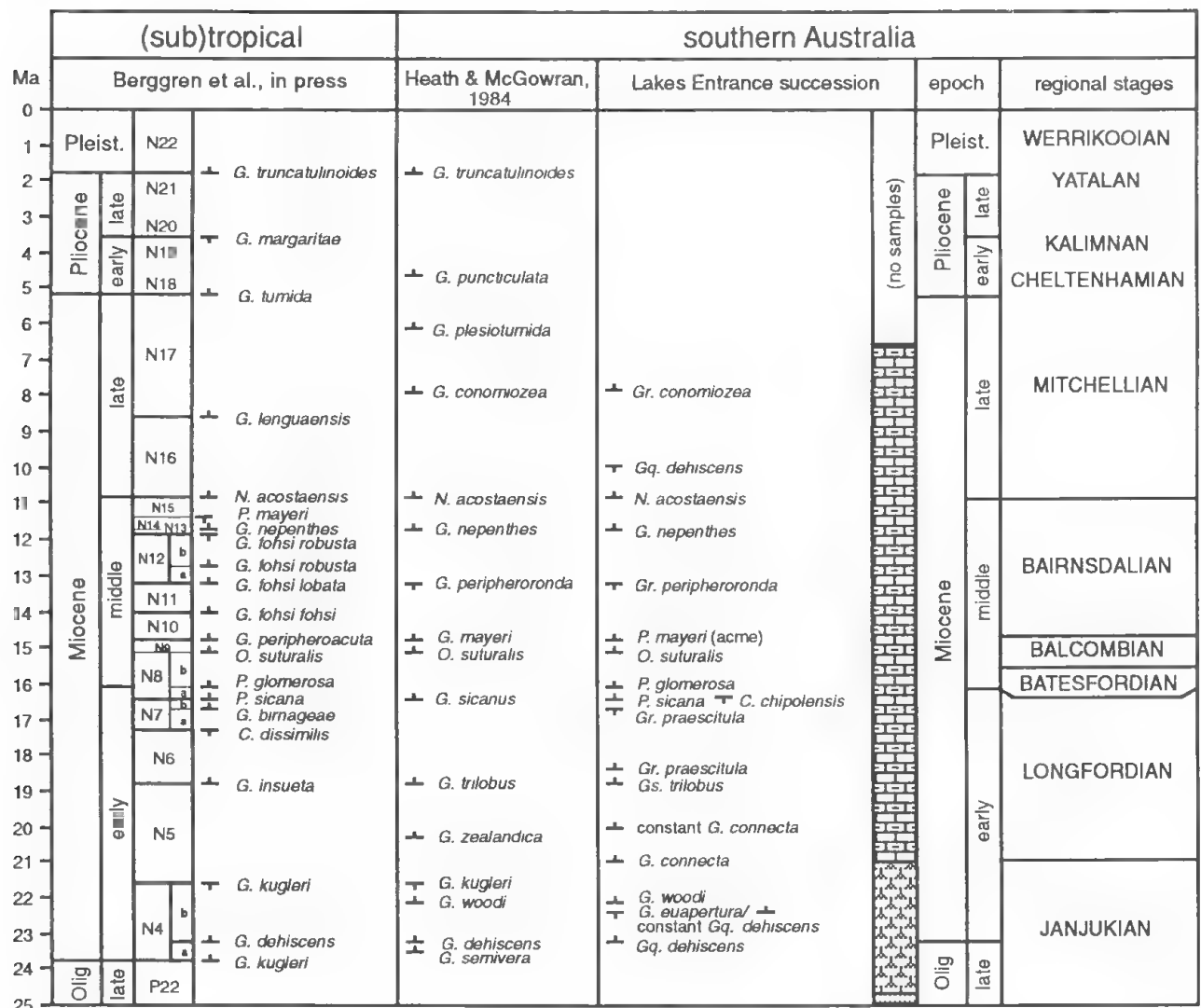


FIGURE 3. The southern Australian planktonic foraminiferal-biostratigraphic succession, shown as first and last appearances (McGowran & Li 1993), is correlated with the standard N-zones of the Neogene (W. A. Berggren, pers. comm. 1992). The regional stages are added at right.

Figure 3 displays a correlation of the local stages with a succession of biostratigraphic events taken from the planktonic foraminifera, which in turn are the main basis for correlation with a standard. Note that local planktonic foraminiferal zones have been abandoned because no consensus was achieved in this terrain of scattered localities and highly composite succession within a greater Tasman region, necessitating continual definition and redefinition of the zones (McGowran, 1978, 1986b; Lindsay, 1981, 1985). Instead, we have sought to compile and improve a detailed sequential ordering of reliable first and last appearances—bioevents or datums, as in Figure 3. At present we are in the uneasy situation of lacking a firm commitment either to routinely used (chronostratigraphic) stages or to stable (biostratigraphic) zones, unlike New Zealand

which has both, with the stages well entrenched (Hornibrook *et al.* 1989). Meanwhile, one of us has developed the habit of thinking of the stratigraphic record in terms of marine transgressions (McGowran 1988), and this might be a basis for a renewed consideration of our local stages, as we discuss below. The more prominent transgressions are listed in Figure 1.

WARM PEAKS AND THE MIOCENE OPTIMUM

It is necessary to develop all possible precision in generalizing about the trajectory of 'climate' through the Miocene oscillation. The marine neritic record at mid-latitudes ought to reflect fluctuations by the comings and goings of pantropical elements, particularly the larger,

phytosymbiont-bearing, benthic foraminifera. And so it has proved. A summary by McGowran (1979, 1986a) concluded that their highly episodic or sporadic distribution in southern Australia was not merely reflecting a sporadic stratigraphic record, a sporadic distribution of suitable facies, or the vagaries of tectonic docking—the Noah's Ark effect. At any rate there were two well-marked intervals of warming with another not so clear and a fourth predicted to fall in the mid-Longfordian but missing, and now to be documented:

(i) The *Operculina*-*Amphistegina* interval, upper Janjukian-lower Longfordian, latest Oligocene-earliest Miocene, equivalent to zones upper P22-

N4. Actually these taxa are mostly successional with the interface at the first appearance of the planktonic *Globoquadrina dehiscens* and at the Janjukian/Longfordian boundary, as Lindsay (1981) pointed out in discussing the lower *Amphistegina* acme, but they do overlap, and the 'interval' includes a window in which the *Globorotalia kugleri* group penetrates to the mid-latitudes. This warm pulse was not seen in the first of the modern Cainozoic oceanic oxygen isotopic profiles (Shackleton and Kennett 1975), which was correlated a little optimistically to the neritic record (McGowran 1979a).

(ii) The addition to the synthesis: Early Miocene,

Lakes Entrance

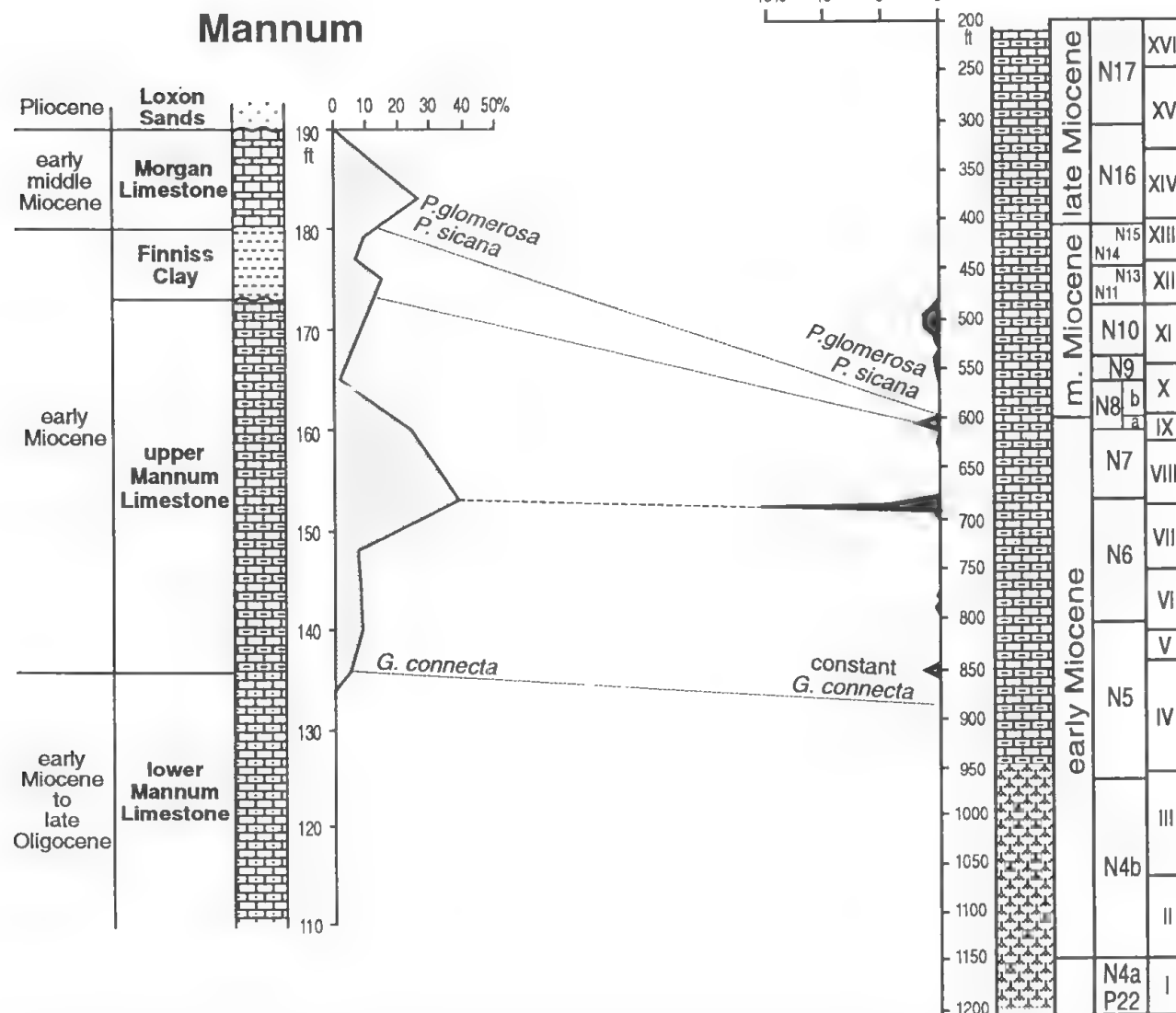


FIGURE 4. Counts of the larger benthic foraminifera *Operculina* and *Amphistegina* in sections at Mannum, western Murray Basin, and Lakes Entrance, Gippsland Basin. Note different scales. Planktonic foraminiferal assemblages I–XVI, from McGowran and Li (1993). This larger foraminiferal horizon in the upper Mannum is between the older Janjukian horizon (but not found in these sections in the lower Mannum), and the younger Batesfordian horizon (the Batesfordian is represented here by the Morgan Limestone, but the larger foraminiferal signature of the climatic optimum has been eroded here).

mid-Longfordian, upper zone N5–N6 equivalent. A well marked peak in the oceanic $d^{18}O$ curve was not matched by a larger foraminiferal spike in southern Australia (McGowran 1979a), even though the oceanic peak was correlated satisfyingly with the *Miogypsina*–*Heterostegina* horizon and the horizon of giant molluscs in the late Eggenburgian of central Paratethys (McGowran 1979b). One miscorrelation of that time, since corrected, was to place the top of the Indo-Pacific stage Te_5 at planktonic foraminiferal zone N8 instead of N6. That error distracted attention from the good record of the spike on the western margin (Chaproniere 1975) if not the southern. Also, Ludbrook's (1961) record of *Austrotrillina* and *Marginopora* in the upper member of the Mannum Formation (western Murray Basin) was overlooked. We have corrected this omission with new records from the Gippsland and western Murray Basins (Fig. 4) showing spikes in the abundance of *Operculina* and *Amphistegina* which both seem to be coeval and to correlate with zone N6. It is noteworthy that the facies are contrasting, for that contrast enhances the importance of the signal as a climatic indicator: at Mannum the plankton counts are very low and *Austrotrillina* and *Marginopora* have been recorded whereas the plankton count is higher and the two genera are missing at Lakes Entrance. This event in southern Australia is a much-subdued version of the warming seen in the later Otaian stage in New Zealand, where tropical-type molluscan and larger foraminiferal assemblages appear in the North Island (Hornibrook 1990).

(iii) Earliest middle Miocene, Batesfordian–Balcombian, Zones N8b–N9. This narrow interval contains two immigrations of *Lepidocyclina*, with *Cyclocypeus* in the east and *Flosculinella* in the west in the younger (Fig. 4), suggesting provincialism—the Austral–Indo-Pacific and the Southeast Australian Provinces (see discussion in Darragh 1985). We have no ready explanation for this provincialism although the large foraminifera are distinguishable ecologically and at least partially distinguishable in their biofacies, as Chaproniere (1975) showed for this region. It is the time of the Batesford–Morgan and the Balcombian marine transgressions and together they display easily the richest warm-water biotic record across southern Australia at the time of maximum Neogene extent of the sea across the continental margins (McGowran 1979a; subsequent discoveries in Lindsay 1981; Benbow and Lindsay 1988). It is the Miocene optimum at

the climax of the Miocene oscillation.

The Miocene optimum has been thoroughly confirmed in Japan and north to Kamchatka, on diverse marine and nonmarine biotic criteria (Tsuchi 1992; Itoigawa and Yamanoi 1990; Gladenkov 1990). The 'tropical marine paleotemperature spike at about 16Ma' (Itoigawa and Yamanoi, 1990) centres on Zone N8b but the concentration of data for warming to high northern latitudes is correlated with zones N8–N9. We see it in the early Badenian transgression and warming in central Paratethys (Steininger and Rögl 1983; McGowran 1979b). Emphasized here as the climatic optimum of the Miocene and the Neogene, it is labelled as climatic optimum 1 in the Pacific oceanic record (Barron and Baldauf, 1990). The second major peak in the Shackleton–Kennett $d^{18}O$ curve (Campbell Plateau) falls at the lower level of this bimodal optimum (McGowran 1979a). The peak is seen at just the 'right' level in New Zealand in the latest Altonian and Clifdenian stages (Hornibrook 1978). A more recent review by Hornibrook (1990) repeats the observations that it is in Altonian time that larger foraminifera (*Lepidocyclina*, *Heterostegina*, *Cyclocypeus*, *Planorbulinella zelandica*, *Amphistegina*) reach southernmost New Zealand; that stenothermal warmwater Indo-Pacific mollusca in the South Island reached maximum diversity (Beu, 1990); and that these records are particularly favoured by the widespread shallow-neritic facies, implying maximum transgression. The Altonian stage extends by correlation from upper zone N6 to about the zone N8a/N8b boundary (Hornibrook *et al.* 1989) but it is clear from Hornibrook's review that the 'thermal maximum' is in the upper Altonian and Clifdenian, i.e. correlated with zones N8–N9.

All of these correlations confirm a distinct peaking of the Miocene oscillation, in a time interval *in toto* of one million years or even less, in the earliest middle Miocene.

(iv) Late middle Miocene, upper Bairnsdalian, Zone N14 equivalents. Not seen in larger foraminifera in southern Australia, this horizon in the Capricorn Basin and New Zealand was correlated with a *Lepidocyclina* horizon in Japan and perhaps with the early Sarmatian marine transgression of central Paratethys (McGowran 1979a,b). Hornibrook (1990) suggests that this temporary warming followed by the extinction of foraminifera in New Zealand is a possibly significant inter-regional event. At Lakes Entrance we find the horizon as an acme in the planktonic *Globigerinoides sacculifer* in Assemblage XIII

(see below; McGowran and Li 1993).]

The warm horizons are shown in Figure 6.

The section at Lakes Entrance in east Gippsland

The Lakes Entrance oil shaft (Crespin 1947) was the one of the very first sections to contribute to our modern understanding of the southern temperate planktonic foraminiferal succession (Jenkins 1960). In reexamining the section, we have used a range of quantified criteria to distinguish sixteen faunal assemblages spanning some 20 Ma (McGowran and Li 1993). The criteria (Fig. 5) include changes in the relative abundances of five species groups approximating clades, the planktonic/benthic ratio, and species diversity. The ratio of the dominant species in the two dominant groups, (*Globigerina woodi* + *connecta*) ÷ (*Globigerina bulloides* + *falconensis*), is a good index of warmer/oligotrophic to cooler/eutrophic changes (shorthand: *woodi/bulloides* ratio). An interesting plot is the actual comings and goings of planktonic species, sample by sample, thus emphasizing the presence (or absence) of a species, not its local range from lowest to highest record.

As we emphasize elsewhere (McGowran and Li

1993), the section falls into three parts. In descending order:

(iii) Assemblages XI to XVI—collapse of the *woodi/bulloides* ratio; measures return to less feverish levels of oscillation. Zones upper N9–N17 equivalents; Bairnsdalian and Mitchellian.

(ii) Assemblages IX to X—greatest amplitudes in fluctuation in all measures including the *woodi/bulloides* ratio. Zones uppermost N7 to lower N9 equivalents; uppermost Longfordian, Batesfordian, Balcombian.

(i) Assemblages I to VIII—decline in planktonic/benthic; rising trends in the *woodi/bulloides* ratio peaking within the mid-Longfordian warm interval; stability in diversity and in incomings and outgoings. Zones N4 to upper N7 equivalents; upper Janjukian to upper Longfordian.

There is an interesting counterintuitive relationship revealed in Figure 5. The positive spikes in the *woodi/bulloides* ratio probably indicate warmings in the upper water column, given what we know of the modern counterparts. If so, then they should match high points both in the planktonic/benthic ratio and in planktonic species diversity. It is consistently clear, however, that the reverse is the case. We suggest as an *ad hoc* speculation that fluctuations in warming were accompanied by increases in precipitation and runoff from the nearby southeastern highlands,

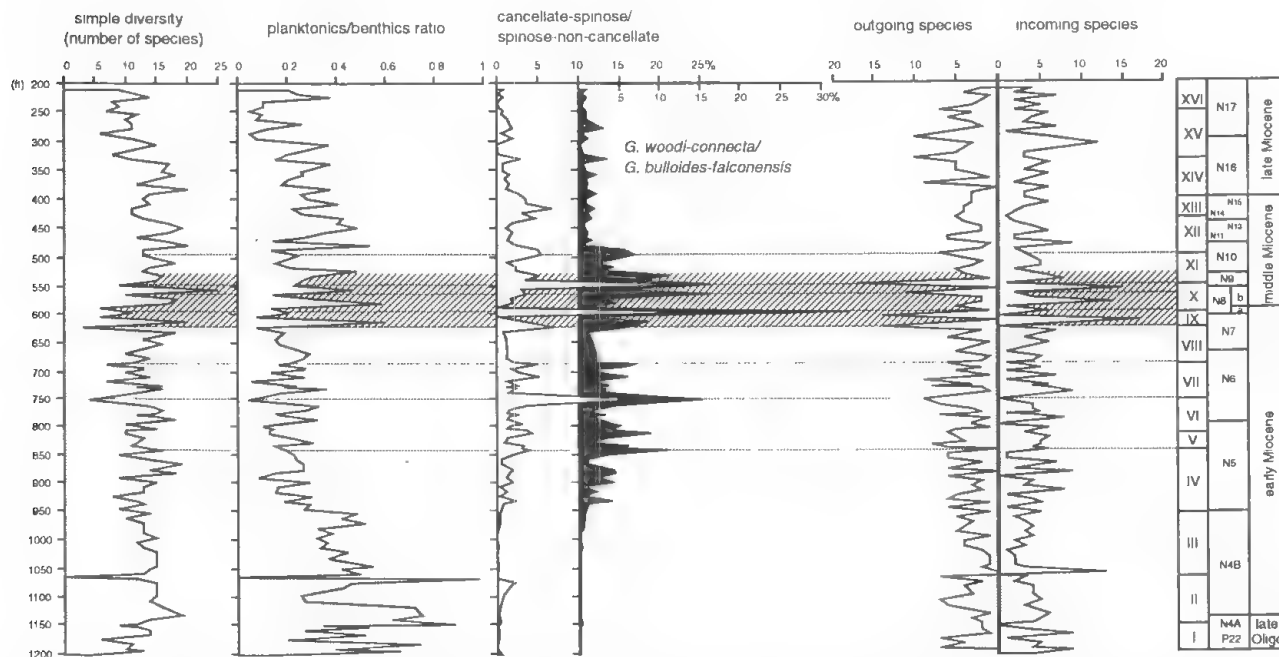


FIGURE 5. Profiles of selected planktonic foraminiferal variables, based on about 15 000 specimens, Lakes Entrance Oil Shaft (McGowran and Li 1993). The *woodi-connecta/bulloides-falconensis* ratio is the dominant component of the cancellate-spinose/spinose-noncancellate ratio. Tie lines emphasize some of the matches, particularly between high *woodi/bulloides*, low diversity and low planktonic/benthic ratio. Hatched interval emphasizes increased oscillations in assemblages IX and X which span the Miocene climatic optimum.

causing briefly an estuarine-type, surface-water outflow, lowering salinity very slightly (planktonic foraminifera are very sensitive to salinity variations) and suppressing both population numbers and taxic diversity. Thus there may be here some evidence of a major increase in precipitation during the climatic optimum, as indeed one would expect.

Correlation: global palaeoceanographic signals

The significance of the Lakes Entrance planktonic foraminiferal succession becomes apparent in the global perspective. Figure 6

displays correlations, independently of each other with the integrated Miocene time scale, of three factors: the Exxon sea level curve (Haq *et al.* 1987); two $\delta^{18}\text{O}$ oceanic profiles which according to Wright *et al.* (1992) reveal glacial fluctuations labelled as the ten *Mi* glaciations; and assemblages I–XVI at Lakes Entrance. Note that at 10^7 years scale there are matches between sea level and palaeotemperature in that both rise to a peak at the optimum, then fall; and at 10^6 years scale there are some matches between glaciation and sequence boundary and some mismatches—a situation that will improve with further scrutiny. Note too that the *Mi* glaciations do not disappear towards the peak of the 10^7 years curve to reappear

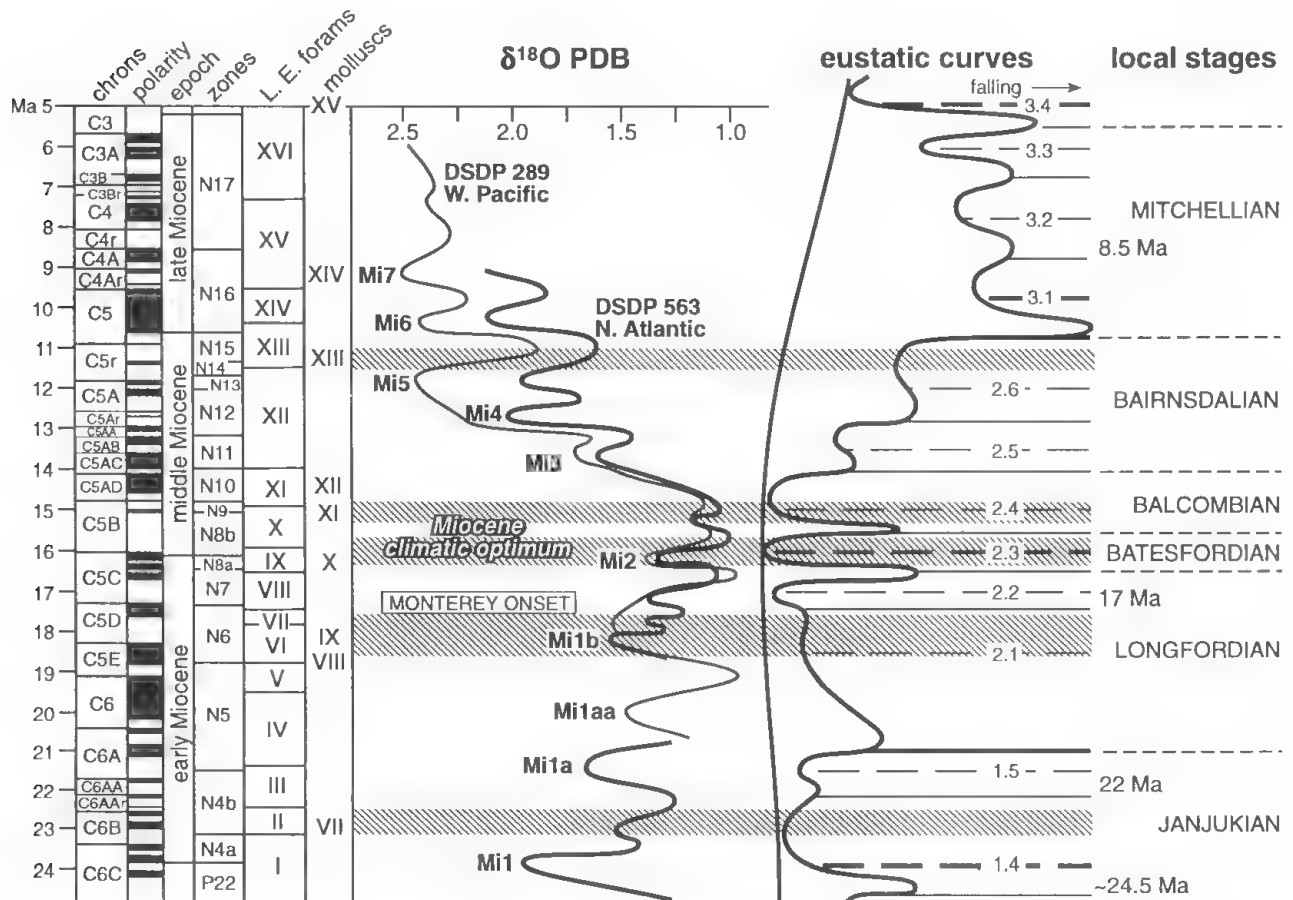


FIGURE 6. Integrated scenario for the Miocene, based on McGowran and Li (1993). Chronology at left, from W. A. Berggren (pers. comm., 1992). Molluscan assemblages VII–XV are from Darragh (1985). The two $\delta^{18}\text{O}$ curves were drawn not by us but by Wright *et al.* (1992) by filtering a cloud of points. The long- and short-term eustatic curves are from Haq *et al.* (1987); solid lines, sequence boundaries broken lines, maximum flooding surfaces with third-order sequence notation. Note that those curves and the planktonic foraminiferal assemblages I–XVI from Lakes Entrance in Gippsland ('L.E. forams') are correlated independently with the time scale, not with each other. Fine tuning will improve the match between *Mi* glaciations and sequence boundaries (solid lines). The regional stage boundaries with integrated geochronology is far from finally fixed. The three warm intervals recognized on the occurrence of larger foraminifera are shown hatched with the Miocene climatic optimum shown as a double, comprising Batesfordian and Balcombian components.

on the downslope, but *Mi2* is close to the summit. This is consistent with the identification of a marine glacial episode during the peak of the Neogene climatic optimum (=Miocene optimum) (Marincovich 1990). Most interesting of all is the sense of increased perturbation in the various measures in assemblages IX and X—at the zeniths of both climatic and sealevel trajectories and preceding, not accompanying, the major falls! It is the Miocene optimum that displays instability in the fossil record, not the immediately subsequent chilling and regression.

Regional stages?

Palaeontologists have long been aware that the Batesfordian and Balcombian stages mark major changes in the molluscan fossil record. That they also mark very brief ages, became apparent in their first correlation with a modern geochronology (McGowran *et al.* 1971). Although Batesfordian facies commonly are bryozoan limestones and Balcombian are marls and clays, there is more to it than merely facies, as Ludbrook (1973) has pointed out. Darragh's (1985) recognition of nine Miocene molluscan assemblages shows an interesting parallel with the planktonic foraminiferal record (Table 1; Fig. 6). Although the tabulation is incomplete, being of 'key' species selected for biostratigraphic significance and not the entire fauna, it shows a major turnover in the Janjukian (greatly exaggerated by a very poor pre-Janjukian record), followed by strong species incomings in both the Batesfordian and Balcombian with disappearances greatly exceeding new arrivals through the Bairnsdalian, then some recovery—partly facies-controlled—in the Mitchellian. Darragh (pers. comm. 1993) warns that taxonomic turnover would be subdued

if the entire assemblages were used, even though his own figure (1985, Fig. 5) gives much the same result. The sense of major molluscan change in the two very short stages at the Miocene optimum deserves study at the full-faunal level.

As stages, erected on molluscan assemblages in neritic facies, become redefined more precisely on planktonic/micropalaeontological criteria (which are external, the organisms having floated in from the ocean), they become rather less useful (Loutit *et al.* 1989). That is because there will always be a problem in recognizing precise bio-events as chrono-events in neritic or paralic facies, where diachronism or erratic preservation and recovery of index fossils are more likely. Instead, suggest Loutit *et al.* we should consider reorganizing stages as depositional sequences, for all strata above a sequence boundary are younger than all strata below it. The notion of 'warm interval' illustrates the problem here. The Janjukian/Longfordian boundary is put at the base of *Globoquadrina dehiscens* which is also close to the first record of the large benthic species *Operculina victoriensis* (Carter 1964, 1990) which is within the warm interval and within 'the difficult transitional period between the Palaeogene and Neogene' (Ludbrook 1973). That necessitated prolonged discussion of the molluscan faunas (Ludbrook 1973) and of the biotic evidence for warming and its chronology (Lindsay 1981), and has contributed to uncertainty in chronology. A possible solution is foreshadowed in Figure 6. It would be better to raise the boundary to the major sequence boundary within the early Miocene so that the macrofaunas and microfaunas could be treated as a unit in local correlation reflecting their unity as a record of the 'warm interval'. That shift upwards would do no violence to boundary stratotypes, for the stratotype Longfordian has no defined lower boundary in

TABLE 1. Nine of the southern Australian molluscan assemblages, with positions in regional stage succession, and first and last appearances of and numbers of 'key species' (i.e. biostratigraphically significant), taken from text and tabulations in Darragh (1985). The assemblages are also shown on Figure 6.

Mollusc assemblage		Stage	First	Last	Total
XV	Bunga Creek	Cheltenhamian	18	10	60
XIV	Rose Hill	Mitchellian	21	5	47
XIII	Lake Bullenmerri	Bairnsdalian	5	41	67
XII	Gunyoung Creek	Bairnsdalian	4	36	99
XI	Balcombe Bay	Balcombian	23	18	116
X	Boornong Road	Batesfordian	25	12	105
IX	Fishers Point	Longfordian	11	10	90
VIII	Jan Juc Beach	Longfordian	9	9	90
VII	Bird Rock	Janjukian	58	34	115

Gippsland and the Janjukian at its stratotype near Torquay has had its upper boundary raised well above the top of the Jan Juc Formation to the bioevent, base *Gq. dehiscens*. Note, however, that that suggestion depends entirely on searching out the sequence boundary 1.5/2.1 in the local strata.

The Longfordian/Batesfordian and Batesfordian/Balcombian boundaries would change little. The Balcombian spans an absurdly brief segment of the *Orbulina* bioseries (Carter 1964) and either it might be subsumed with the Batesfordian as substages of a Balcombian *sensu lato*, as Carter (1990) has proposed, or it could occupy cycle 2.4. The Bairnsdalian/Mitchellian boundary would change little. The point is that the concept of the local or regional stage would change for the better, and they would return to routine and widespread use as natural divisions of the stratigraphic record, should a comprehensive sequence-stratigraphic analysis cogently identify the boundaries. Meanwhile, we emphasize again that the regional stage boundaries shown in Figure 6 are suggestions, not conclusions.

DISCUSSION

The Miocene succession in southern Australia can be compared closely with a global scenario of rising sealevels and temperatures from the latest Oligocene to the early middle Miocene, then a pronounced plunge in both indicators from the early middle Miocene to the late Miocene. The generalized stratigraphic patterns in Figure 2 are in accord with the trends in Figure 6. Superimposed on these broader (10^7 years) trends are the higher-frequency phenomena detected in the oceanic oxygen isotopic record, the third-order depositional cycles, and the local planktonic foraminiferal assemblages—all at *comparable* time scales in the 10^6 year band. But where we find numerous 'warm intervals' in the planktonic foraminiferal *woodi/bulloides* ratio at that frequency, we see only three warm intervals in the Miocene on more comprehensive criteria as well as at a longer time scale. They are in the Janjukian–early Longfordian, the mid-Longfordian, and the Batesfordian–Balcombian, the last being the twin-peaked Miocene climatic optimum. It is likely, but only partly indicated on Figure 6 and yet to be rigorously established, that the mini-glaciations *Mila* and *Milaa* will fall between the first and second of these warm intervals, and *Milb* and *Mi2* between the second and third. When it was warmer, it was wetter, and that too may be seen at the higher frequency in the

woodi/bulloides ratio.

What have these generalizations to do with the terrestrial biotic record? There are several implications:

(i) The regional patterns have extensive good matches with the global patterns. Therefore, we would be very suspicious of arguments that attempt to contrast a drier interior with a more humid coast, say, or a milder south with a warmer north. It is not that those contrasts did not exist—they did!—but that the chronologies and correlations are too weak to permit separation of lateral contrasts from vertical contrasts. The signals from the oceanic and neritic records will have their counterparts continent-wide in the various components of the environmental mosaic, obscure though they probably are. For example, a warming will be signalled coevally in three ways in three environments—as a $\delta^{18}\text{O}$ negative kick in the oceanic realm, as an immigration from the tropics in the (expanded) neritic realm, and as a change from drier to moister floras in the terrestrial realm.

(ii) However, arguments about environment or evolution have to be at the right time scale and relative ages have to be correct at that scale. If chronological correlations of two faunas or floras are wrong by a million years, then comparisons and contrasts depending on a perceived contemporaneity become nonsensical, because the environment is oscillating at that same scale which is too fast for any generalization to mean anything. There is little to be said about (for example) two 'late Oligocene–early Miocene' faunas in this context because we simply do not know whether they were coeval or not.

(iii) However, more can be said at the longer scale—comparing early-middle Miocene faunas or floras with middle–late Miocene, for example. In 1983–84 there were no Miocene marsupial faunas (other than *Wynyardia*) recognized as being older than Batesfordian in Australia (Woodburne *et al.* 1985). By 1992–93, there had been a substantial downward revision of several, so that the early Miocene and late Oligocene is now populated with assigned terrestrial assemblages (Archer *et al.* 1989, 1994; Rich *et al.* 1992; Megirian 1992; Woodburne *et al.* 1994). That is intrinsically a more likely scenario of age distributions, because it shifts some of the more important terrestrial faunas into *generally* warmer–wetter times, which are more likely to be preserved (and discovered) than are the biotas of cooler–drier times (McGowran 1986b). It is unlikely on predictable environmental grounds that the Riversleigh

assemblages are Bairnsdalian, as Woodburne *et al.* (1985) suggested.

(iv) There has been some disagreement over the broad nature of the Riversleigh environments. The host sediment, the Carl Creek Limestone, has been interpreted as a calciclastic alluvial outwash that could only have accumulated under relatively dry and perhaps even semi-arid conditions (Megirian 1992). That implies to Megirian that the Riversleigh rainforest was merely a refugium and the high mammalian diversities in the Miocene are due to the mixing-in of biotas from much drier distal habitats. Archer *et al.* (1994) advance several ecological and taphonomic arguments against this view and reiterate earlier conclusions that the Riversleigh assemblages represent biotas in low-latitude rainforests. Our emphasis on the distinction between phenomena at 10^7 and 10^6 year scales might point to a resolution of this conflict by accommodating both scenarios at the higher frequency. Thus the preserved faunas might be biased in their age distribution towards the warmer-wetter segments of Longfordian–Balcombian times when the terrain was heavily forested and the limestones were karsted. The sedimentological evidence for the depositional environment of the Carl Creek and equivalent limestones might be biased towards the *Mi* glacial (=cooler/drier) times of the same time span. Several successional and alternating episodes of the contrasting environmental regimes could easily be accommodated within the age range of the Riversleigh.

(v) Those revisions in the correlation and age determination of vertebrate assemblages also

accord better with emerging generalizations about Australian floras. Whereas macrofloras are more informative than microfloras as to environment, too often they are poorly constrained in their geological ages, so that an entire discussion can become diffuse as to what happened and just when did it happen (e.g. Hill 1992). On microfloral evidence mostly from the eastern Murray Basin, Martin (1989) concludes that the region largely was forested and mostly with rainforest prior to the middle Miocene. In the middle-to-later Miocene widespread rainforest was extensively replaced by eucalypt wet sclerophyll forest. The extent of moist forest and deep chemical weathering predictably reached their maximum during the Batesfordian–Balcombian climatic optimum. The later Miocene was somewhat drier, and we can now assert that a change toward drier sclerophyll forests would have begun fairly early in the middle Miocene, in the early Bairnsdalian, *sensu* Figure 6. On Martin's recent studies pertaining to the problem of Australian grasslands, Archer *et al.* (1994) comment: 'On balance, there is no evidence for early to mid Miocene grasslands in Australia'—a generalization that has the right 'feel' about it from our standpoint. The subsequent change in vegetation also entails a change towards sparser records, and records that are harder to date with confidence and precision.

The Monterey effect?

Why did the world warm up through the early Miocene, teeter on the brink for about a million

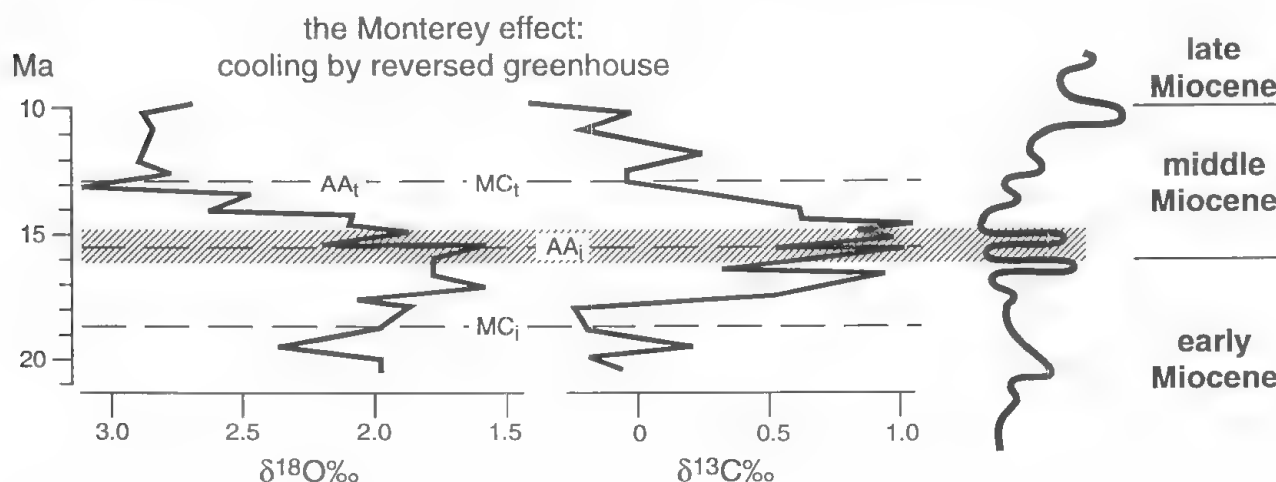


FIGURE 7. The isotopic patterns demonstrating the Monterey effect operating over several million years (Vincent and Berger 1985). MC_i, MC_t, Monterey carbon event, initiation and termination. AA_i, AA_t, Antarctic ice buildup, initiation and termination. Eustatic curve as for Figure 6. Hatching shows the Miocene climatic optimum, identified on other grounds (see text and Figures 5 and 6) but most importantly fitting the pattern very well by correlation.

years, then plunge toward the chilly state of the late Neogene, never again to attain that greenhouse state of fifteen million years ago? The Monterey hypothesis of Vincent and Berger (1985) still fits the record well. It is a pattern hypothesis in which the profiles of $d^{13}C$ and $d^{18}O$ reveal cause and effect (Fig. 7). A pronounced positive trend in $d^{13}C$ beginning at horizon MC_1 was found in both surface and bottom oceanic successions, suggesting removal of light carbon from the oceanic reservoir (such as into the organic-rich Monterey Formation and its circum-Pacific equivalents). At a critical point, the $d^{18}O$ trend, strongly negative, went suddenly into the opposite direction, indicating growth of the Antarctic icecap and chilling of the global bottom waters at a CO_2 drawdown, a threshold in

reversed-greenhouse (AA_1). The event concluded after about 5m.y. at horizons MC_1 , AA_1 . It all fits very well chronologically with the Miocene climatic optimum with its attendant evidence from sea level and the fossil record.

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WORLD HERITAGE AND FOSSILS

MARY JINMAN

Summary

The purpose of this paper is to give a broad overview of the World Heritage Convention, to explain Australia's participation and to give details of the first Australian Fossil Site nomination : Murgon, Riversleigh and Naracoorte.

WORLD HERITAGE AND FOSSILS

The purpose of this paper is to give a broad overview of the World Heritage Convention, to explain Australia's participation and to give details of the first Australian Fossil Site nomination: Murgon, Riversleigh and Naracoorte.

The Convention Concerning the Protection of the World's Natural and Cultural Heritage, known as the World Heritage Convention, was adopted by the UNESCO General Conference in 1972. In 1974, Australia became one of the first signatories. Since then, the number of countries that are party to the Convention has risen to 132.

The World Heritage Convention aims to promote co-operation among nations to protect worldwide heritage which is of such universal value that its conservation is a concern of all people. It is intended that, unlike the seven wonders of the ancient world, properties will be conserved for all time. Member countries commit themselves to ensuring the identification, protection, conservation, presentation and transmission to future generations of their World Heritage Properties. These ideas form the very backbone of the Convention.

The Convention establishes the World Heritage List, which identifies natural and cultural properties considered to be of outstanding universal value, and, by virtue of this quality, especially worth safeguarding for future generations. In order to qualify for inscription on the World Heritage List, a nominated property must meet specific criteria and integrity conditions from either a natural or cultural point of view.

The world's natural heritage offers a priceless legacy. It includes sites representing major stages in the geological and biological history of the earth; outstanding examples of significant ongoing processes; areas of exceptional natural beauty; and significant natural habitats for the conservation of biodiversity. Examples of natural properties include Sagarmatha National Park in the Himalayas of Nepal and Iguacu National Park, a cross border listing shared by Brazil and Argentina.

Cultural heritage sites are equally priceless. Certain archaeological sites, groups of historic buildings, ancient towns, monumental sculptures and paintings whose significance transcends political or geographical boundaries constitute part of this irreplaceable heritage. Some of these treasures represent unique artistic achievements and masterpieces of the creative genius; others

have exerted great influence over a long period of time or within a cultural area of the world. Some may be the unique witness to a civilisation which has disappeared or to a type of settlement that has become vulnerable under the impact of change. Others may be associated with ideas or beliefs that have left an indelible mark on the history of humanity. Cultural heritage covers a wide range of properties, including the Tassili n'Ajjer in Algeria and the Vezelay Abbey in France.

A World Heritage Property can be listed for both natural and cultural values. Even so, the division between natural and cultural properties is somewhat artificial, and in the last year has been addressed to some extent with the addition of cultural landscapes as a group over the middle ground.

An essential characteristic of the World Heritage properties is their variety: without the multiplicity of animal and plant species and the diversity of ecosystems, without the distinctive contributions of every culture and every people, the immense tapestry would remain incomplete.

To date, Australia has ten World Heritage properties, which all contribute significantly to the wealth of the tapestry. Australian World Heritage properties read like a travelogue of our most spectacular and unique places and include:

- the Great Barrier Reef
- the Willandra Lakes Region
- the Lord Howe Island Group
- Uluru National Park
- the Wet Tropics of Queensland
- East coast temperate and subtropical Rainforest parks
- the Tasmanian Wilderness
- Shark Bay
- Kakadu National Park
- Fraser Island.

All of Australia's properties have been listed for their natural values and are generally very large. We have the honour of having four properties listed on all four natural criteria, and three listed for both natural and cultural criteria. This puts our properties into a very elite group.

Australia has been very active in the World Heritage field, not only with the listing of our properties, but also with their protection. In 1983, the Commonwealth Government enacted the *World Heritage Properties Conservation Act*, which provides for the protection and conservation

of World Heritage Properties in Australia and its external territories.

There are now 380 sites on the World Heritage List, which includes several fossil sites:

- the Burgess Shale site in Canada,
- the Dinosaur Provincial Park in Canada,
- and Olduvai Gorge in Tanzania.

Australia has a fossil record of great antiquity, extending from 3.5 billion years ago to the present.

On 21 December 1992, the Prime Minister, Mr Keating announced in his Environment Statement that the fossil sites at Riversleigh and Naracoorte would be nominated to the World Heritage List in 1993. The Murgon Fossil site will also be included in the nomination. Agreement has been reached with the South Australian and Queensland Governments to proceed with the nomination.

The three sites represent three key stages in the evolution of our unique Australian fauna over the last 55 million years.

The marsupial fossils from Murgon include a diverse suite of primitive forms, some of which appear to more closely resemble extinct South American marsupials than any previously known from Australia. Besides marsupials, many other discoveries have been made, including the tiny tooth of a very small placental mammal, which is challenging understanding about the evolutionary and biogeographic history of this region of the world. The site is about 55 million years old, and is the only link between the opalised monotreme jaw from Lightning Ridge in NSW and younger mammal deposits.

The Riversleigh deposits date from 25 million years old to the present, and occur in unique freshwater limestone. With more than 20 000 specimens representing 150 faunal assemblages, Riversleigh has led to an understanding of how the environment and the animals that lived in it have changed over time from a rich rainforest community to a semi-arid grassland.

The fossil bed and Ossuaries of Victoria Fossil Cave at Naracoorte contain the remains of at least 93 vertebrate species, ranging from tiny frogs to buffalo sized marsupials. This makes it one of the

richest Pleistocene marsupial fossil deposits in the world. The sediments accumulated between 170 000 and 18 000 years ago and therefore over two of the Pleistocene glacial periods.

As the sites occur in two different States, the Commonwealth Government is responsible for preparing the nomination documents in close consultation with the States involved. Nominations must be submitted to the UNESCO secretariat in Paris – by 1 October each year. They are then referred to the World Heritage Bureau (the executive of the Committee) and thoroughly assessed. The Bureau is assisted in this task by IUCN – the World Conservation Union which advises on natural sites and ICOMOS which advises on cultural sites. In addition, these organisations consult with relevant experts around the world.

The evaluations are considered by the Bureau at their meeting in the year following the submission of the nomination, and a recommendation on the listing of the property is made to the World Heritage Committee. The Committee consists of 21 nations and represents the different regions and cultures of the world. It considers the recommendations from the Bureau and the evaluation from IUCN or ICOMOS and decides whether the property will be inscribed.

For the Australian Fossil Sites nomination being prepared this year, this timetable will mean the nomination is submitted by October 1993, assessed in early 1994, considered by the Bureau in June 1994 and a decision made by the World Heritage Committee in December 1994. As can be seen, World Heritage Listing is not an instant process and usually takes about two years to complete.

This fossil sites nomination seeks to tell a story of change over time, rather than just providing a snapshot of the sites. There is potential if this nomination succeeds, to nominate further sites that fill out the story of mammal evolution in Australia, or tell other unique stories of universal value. World Heritage attracts a lot of attention, and the 1993 nomination of Australian Fossil Sites will increase worldwide awareness of our unique Australian history.

PROTECTION OF MOVABLE CULTURAL HERITAGE

PHIL CREASER

Summary

The Commonwealth Protection of Movable Cultural Heritage Act 1986 was enacted in 1986 and brought into operation in 1988. The principal goal of the program is, as stated in November 1985 in the Federal Parliament by the then Minister for the Arts, Heritage and the Environment, the Hon. Barry Cohen MP, 'to protect Australia's heritage of cultural objects and to extend certain forms of protection to the cultural heritage of other nations' through controls on the export and import of significant movable cultural heritage objects. A closely related goal was to enable Australia to accede to the 1970 UNESCO Convention on the Means of Prohibiting and Preventing the Illicit Import, Export and Transfer of Ownership of Cultural Property.

PROTECTION OF MOVABLE CULTURAL HERITAGE

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Probably the most important aspect of the Act is the National Heritage Control List, which defines the categories of movable objects that are classed as 'Australian protected objects'. The Control List includes Class A objects which cannot be granted a permit for export and Class B objects that may be granted a permit for export.

Class A objects include some of the most significant items of Aboriginal heritage:

- bark and log coffins;
- human remains;
- rock art; and
- dendroglyphs (carved burial and initiation trees).

Class B objects include:

- archaeological objects;
- other objects of Aboriginal heritage;
- archaeological and ethnographic objects of non-Australian origin;
- natural science objects of Australian origin;
- objects of applied science or technology;
- military objects;
- objects of decorative art;
- objects of fine art;
- books, records, documents, graphic material and recordings;
- numismatic objects;
- philatelic objects; and
- objects of social history.

The Control List also sets out the particular criteria defining 'Australian protected objects' in each category controlled under the Act. Generally the criteria include historical association, cultural significance to Australia, representation in an Australian public collection, age and current Australian market value.

The Act also provides for the establishment of the National Cultural Heritage Committee whose main function is to advise the Minister on the operation of the Act. The Committee consists of ten people of whom four represent collecting institutions, four have experience relevant to the cultural heritage of Australia, one is a nominee of the Minister for Aboriginal Affairs and one is a member of the Australian Vice Chancellors Committee.

The day-to-day administration of the Act is carried out by the Cultural Heritage Branch of the Department of the Arts and Administrative Services. The most common aspect of the administration of the Act is the process for the issuing of export permits.

It is important to stress that within each category there is a definition of whether or not the item comes under the Act. For example, a palaeontological object must have an Australian market value of more than \$1 000 before it comes under the Act. Similarly, a mineral must have a value of \$10 000. However all meteorites and australites are covered under the Act. In many cases, the item does not come under the Act. If, however, the item is a 'protected object' it will be necessary to obtain the relevant form from the Branch for the export of the item.

When the completed form is returned to the Branch, it is then sent to Expert Examiners who assess the application. These examiners are usually from collecting institutions who have a good knowledge of the item in question and similar items elsewhere in the country. The reports from the Expert Examiners are then forwarded to the Committee for consideration. The Committee, in turn, makes its recommendation to the Commonwealth Minister—at present, Senator the Hon. Bob McMullan—who duly decides on whether a permit should be granted. One important point to note is that the Committee does not have to abide by the reports from the examiners and the Minister does not have to accept the Committee's recommendation, i.e. the Minister makes the decision. The time taken for this process can range from a few days to few months, particularly if the item is of major significance.

To date, over 160 applications for an export permit have been received by the Department and only one item, a painting, 'The Bath of Diana', has been refused an export permit.

One other important aspect of the Act of interest to palaeontologists is the topic of illegal exports.

The export of fossils with a value of \$1 000⁵ or more from Australia is prohibited under the Act if a permit has not been obtained. The maximum penalty for this offence is a \$100 000 fine or imprisonment for five years, or both.

Following a request from this Department in mid-1991, the Australian Federal Police began inquiries into the alleged theft of Ediacaran fossils from South Australia. These inquiries resulted in the identification of a number of suspects. The investigation also identified further sites in South Australia and Western Australia where fossils had been removed and in late October 1991, the Australian Customs Service in Perth intercepted a suspect allegedly attempting to smuggle fossils out of the country. A number of fossils were seized which police believe were intended for sale on overseas markets. The police are continuing their inquiries and some fossils which have been illegally exported have been returned to Australia. It is not possible to provide all the details of this case as the investigation is still to be finalised.⁵

A review of the Act was conducted recently to evaluate the efficiency and effectiveness of the cultural heritage export and import control program, established by the Act and Regulations. The review report was released as a discussion paper. Government departments and authorities, interested organisations and the general public were invited to comment on the report and its recommendations and ninety-two submissions were received. The major issues addressed in the report included:

- publicity for the scheme;

- devolution of the centralised system of administration of the scheme to the collecting institutions in the States and Territories;
- amendments to the Control List including the creation of a 'National Register';
- overcoming the lack of money in the National Cultural Heritage Fund.

A total of 60 recommendations were made in the report, some of which require changes to the Act. Of particular interest to palaeontologists is the recommendation to remove the \$1 000 minimum market value on palaeontological objects. If accepted, this will mean that all fossils will come under the ambit of the Act. A report will be presented very shortly to the Minister which addresses these recommendations in terms of the public response, the views of the Committee and the department perspective. Depending on ministerial decisions, there may be some amendments to the Act and some changes to the administration of the scheme.

Movable cultural heritage is a complex topic. There is a need for the Act to be administered in a very understanding way and for policies to be developed which reflect current trends and financial positions. However, it could be considered that awareness of the scheme by individuals as well as collecting institutions is the most important issue that needs to be addressed. In this regard, a mailing list is being compiled of all those with an interest in this topic.

With an increasing awareness of the scheme, we are confident that there will be an increasing awareness of the value of our cultural heritage, including our palaeontological heritage.

Phil CREASER, Cultural Heritage Branch, Department of the Arts and Administrative Services, G.P.O. Box 1920, Canberra, Australian Capital Territory 2601. *Rec. S. Aust. Mus.* 27(2); 215–216. 1994.

⁵ On 3 August 1993, the Regulations under the Act were amended and the \$1 000 minimum value for palaeontological objects was removed. This means that a permit is required before any fossil specimen is exported. Following a Cabinet reshuffle on 28 January 1994, the Hon. Michael Lee, Minister for Communications and the Arts, assumed responsibility for the Act and administration of the scheme. At that time, the number of applications for permits had increased to more than 220 with the majority of recent applications being for fossils. In addition, one further item, an historic steam engine, has been refused an export permit.

**ABSTRACTS OF THE FOURTH CONFERENCE ON AUSTRALIAN
VERTEBRATE EVOLUTION, PALAEOONTOLOGY AND SYSTEMATICS,
ADELAIDE, 19-21 APRIL, 1993**

ARCHER, M., GODTHELP, H., MUIRHEAD, J., NOCK, C., & AUGEE, M. 1994
*School of Biological Sciences, University of New South Wales, Kensington,
New South Wales, 2033.*

Summary

Discovery in late 1990 of a single upper molar of an early Paleocene monotreme by palaeontologists from the University of La Plata (including Rosendo Pascual and Edgardo Ortiz Jaureguizar) led to the description of *Monotrematum sudamericanum* (Pascual *et al.* 1992). An invitation from the Argentinians to mount a joint expedition from the University of New South Wales was taken up with the aid of a substantial financial grant from the Australian Geographic Society and equipment donated by Paddy Pallins of Sydney. In November and December 1992, we combined efforts to investigate early Paleocene Banco Negro Inferior exposures at Punto Pellegro north of Comodoro Rivadavia, Argentina. The results were highly successful. In addition to more ornithorhynchid material, marsupials, condylarths, enigmatic mammals and colossal leptodactylid frogs were found on eroded surfaces and in quarries. Exploration of late Mesozoic to Oligocene sediments in the Grand Baranca, near Sarmiento (west of Rivadavia Comodoro) was equally productive and provides, with the Punto Pellegro deposits, a significant opportunity to expand understanding about the earliest Cainozoic mammal record of South America.

**ABSTRACTS OF THE FOURTH CONFERENCE ON AUSTRALASIAN VERTEBRATE
EVOLUTION, PALAEOONTOLOGY AND SYSTEMATICS,
ADELAIDE, 19-21 APRIL 1993**

In pursuit of the peregrinating Patagonian platypus

ARCHER, M., GODTHELP, H., MUIRHEAD, J., NOCK, C. & AUGEE, M. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

Discovery in late 1990 of a single upper molar of an early Paleocene monotreme by palaeontologists from the University of La Plata (including Rosendo Pascual and Edgardo Ortiz Jaureguizar) led to the description of *Monotrematum sudamericanum* (Pascual *et al.* 1992). An invitation from the Argentinians to mount a joint expedition from the University of New South Wales was taken up with the aid of a substantial financial grant from the Australian Geographic Society and equipment donated by Paddy Pallins of Sydney. In November and December 1992, we combined efforts to investigate early Paleocene Banco Negro Inferior exposures at Punto Pellegro north of Comodoro Rivadavia, Argentina. The results were highly successful. In addition to more ornithorhynchid material, marsupials, condylarths, engimatic mammals and colossal leptodactylid frogs were found on eroded surfaces and in quarries. Exploration of late Mesozoic to Oligocene sediments in the Grand Baranca, near Sarmiento (west of Rivadavia Comodoro) was equally productive and provides, with the Punto Pellegro deposits, a significant opportunity to expand understanding about the earliest Cainozoic mammal record of South America.

Australian VP bibliography computer data base

BAYNES, A. 1994

Department of Earth and Planetary Sciences, Western Australian Museum, Perth, Western Australia 6000.

The first version of the VP bibliography computer data base was created by combining the Australian mammal chapter bibliography and appendix (in which mammal genera are indexed to the papers) from the then-unpublished *Vertebrate Palaeontology of Australasia*. It is available in Macintosh and PC versions, and its purpose is to answer the question 'What is the literature on genus *x*?' It was offered free on a flyer in *VP of Australasia*. The response was, frankly, lousy. Undismayed, I am expanding it into the MARB (Mammals Amphibia Reptiles & Birds) Australian VP bibliographic data base. In MARB both the process of extracting references to a mammal genus and the indexing of mammal genera mentioned in a paper are simpler. Such a data base can potentially be perfected for the older references with complete generic indexing, and the references can always be cited without error. It can also be kept up-to-date much more easily than a reference book. By CAVEPS, MARB will include the papers but not the indexing of the ARB genera. For these expert help is needed. Graduate students probably represent the best source of manpower for completing the indexing and adding new references, as they will be making the greatest use of the data base. I am hoping someone else will do one on fossil fish, which I know nothing about.

The MARB data base was demonstrated at CAVEPS 93. Copies are available: free to those who contribute to it; \$10.00 (or \$11.00 including the disk) for others.

Preliminary analysis of mammals from Allens Cave, southern NullarborBAYNES¹, A. & WALSHE², K. 1994

1. Department of Earth and Planetary Sciences, Western Australian Museum, Perth, Western Australia 6000.
2. Department of Archaeology and Anthropology, The Faculties, Australian National University, Canberra, Australian Capital Territory 2601.

Archaeological excavations made in Allens Cave in 1989 yielded substantial quantities of bones. Those from pit E4 (1 m²) have been analysed. The stratigraphy consists of a basal orange unit 1.9 m deep terminating in a gravel lag deposit that marks a disconformity; above this is a 1.4 m dark grey unit. Two radiocarbon dates have been obtained: 3 720 ± 150 yrs BP at about 1.1 m depth and 5 860 ± 430 yrs BP at the base of the dark grey unit. The orange unit is currently undated, but probably late Pleistocene in age. Remains of large mammals are generally highly fragmented; those of the smaller mammals are dissociated but more complete. Burnt bone is present at all levels. These observations suggest that the principle agents of accumulation were owls (*Tyto* spp.), devils and humans. In the orange unit the contribution from devils and humans predominated; in the dark-grey unit there is more substantial owl prey component.

The mammal fauna of the orange unit is restricted to species whose original distributions include the most arid parts of modern Australia. Above the disconformity species richness increases with the addition of some arboreal species and a substantial south-western element, but few losses. These faunas suggest very arid conditions at the time of deposition of the orange unit and higher rainfall during deposition of the dark grey unit. This is consistent with vegetation changes inferred from palynological investigations of this and other southern Nullarbor deposits.

Responses of mammalian communities to late Quaternary climatic changesBAYNES¹, A. & WELLS², R. T. 1994

1. Department of Earth and Planetary Sciences, Western Australian Museum, Perth, Western Australia 6000.
2. School of Biological Sciences, Flinders University of South Australia, Bedford Park, South Australia 5042.

Compared to North America, Australia still has very few windows opened on what was happening to mammalian communities in the geologically recent past. The principal southern and western sites are Devils Lair and Skull, Hastings, Allens, and Victoria Caves. All analysed large stratigraphically discrete samples of mammals show log-normally distributed rank-abundance distributions, indicating that a number of communities has been sampled by agents accumulating remains in the caves, as would be expected. In only one or two cases has an attempt been made to resolve the mammals from a deposit into their contemporary communities; the other sites merely provide assemblage data. The small to medium-sized mammal assemblages from the sites reflect different species equilibria in local mammal communities at different times in the glacial-interglacial cycle. The sites in temperate and semi-arid areas show greater species richness in glacial age deposits than in later Holocene deposit the so-called disharmonious assemblages effect. In marked contrast, in Allens Cave, located on the edge of the modern arid zone but close to the Southern Ocean coast, the higher species richness is in the Holocene levels. This pattern is consistent with the idea that species richness is higher at times of more equable climates. As climates become more equable increasing numbers of species appear to have been integrated into more complex communities. As climates changed in the opposite direction faunal segregation has resulted in simpler communities. The general pattern is also consistent with a centrifugal movement of faunas in response to extremes of continental glacial aridity.

New species of *Nambaroo* (Flannery and Rich) from Riversleigh, northwestern Queensland.

COOKE, B. N. 1994

School of Life Science, Queensland University of Technology, Brisbane, Queensland, 4001.

New species of *Nambaroo* (Flannery and Rich, 1986) are described from a variety of sites of estimated early to mid-Miocene age from Riversleigh deposits of northwestern Queensland. The new species are phenetically similar to those described by Flannery and Rich (1986) from the mid-Miocene Namba Formation of South Australia. Their lower molar morphology supports the views of those authors regarding the evolution of the hypolophid and posterior cingulum among macropodids.

Pliocene whales and dolphins (Cetacea) from the Vestfold Hills, AntarcticaFORDYCE¹, R. E. & QUILTY², P. G. 1994

1. University of Otago, Dunedin, New Zealand.

2. Australian Antarctic Division, Kingston, Tasmania, 7050.

Early Pliocene cetaceans from Marine Plain, Vestfold Hills (68°35'S, 78°00'E), are the only fossil higher vertebrates known so far from the Antarctic Oligocene-Pleistocene. Of these, one (possibly two) undescribed extinct species of dolphin (Odontoceti: Delphinidae: new genus) is known from skulls, mandibles, ear bones, and post-cranial elements from three individuals. Skull bones have contact relationships similar to those in other delphinids, but skull topography is remarkably convergent with some extant toothless beaked whales in the genus *Mesoplodon* (Odontoceti: Ziphiidae): the narrow rostrum is toothless, there is a prenasal basin, and the premaxillae carry flat vertical flanges beside the nares. The dolphins seems too derived to be ancestral to any extant species; otherwise, relationships to extant delphinids are uncertain. The shallow marine depositional setting at Marine Plain cautions against but does not preclude ziphiid-like habits (pelagic, deep-diving, semi-solitary, squid-eating) for the dolphin.

Of other specimens, an articulated series of large vertebrae is probably from a baleen whale (Mysticeti). A small right whale (Mysticeti: Balaenidae: genus and species uncertain) has a narrow and ventrally curved but otherwise poorly preserved rostrum and a fragmentary braincase. Ear bones from this specimen, when fully prepared, should better reveal relationships. The fossils are unexpected in that small dolphins (or small ziphiids) and small right whales appear ecologically insignificant in near-shore modern Antarctic waters. Indeed, late Neogene Cetacea elsewhere include bizarre forms and/or unusual distributions, as well as species and distributions of modern aspect. These unusual taxonomic and ecological patterns apparently did not persist into the Pleistocene, which suggests a later Pliocene shift in global cetacean ecology.

Cuddie Springs: new light on Pleistocene megafaunaFURBY¹, J. & JONES², R. 1994

1. School of Geography, University of New South Wales, Kensington, New South Wales, 2033.

2. Department of Palaeontology, Australian Museum, Sydney, New South Wales, 2000.

The faunal list for the Cuddie Springs site (compiled after excavations in 1993) has been expanded to include an additional 11 taxa following excavations during 1991. Pollen and sediment analysis has provided a palaeoenvironmental record spanning the late Pleistocene, including the period when the megafauna disappeared. The vegetation history from Cuddie Springs has a time depth not previously recorded from arid-semi-arid contexts. Archaeological material at depth was first documented in the recent excavations with aboriginal stone artefacts occurring in direct association with bones of *Genyornis*, *Diprotodon* and *Sthenurus*, dating to about 30 000 years B.P. The faunal record is continuous to at least five metres depth and one of the aims of ongoing research is to document the changes in the faunal assemblage through time in an environmental context.

Some rodents from the Pleistocene fluviatile deposits of the eastern Darling Downs, Queensland

GODTHELP, H. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

Sediments collected from several sites on the Eastern Darling Downs were washed and sorted. The fossilised remains of many vertebrates were recovered. The assemblages were dominated by the remains of murid rodents; 8 taxa are recognised. One taxon is as yet unidentified and may represent a new species of *Pseudomys*, the remaining are all extant species. *Mastacomys fuscus* and *Pseudomys higginsii* are recorded from Queensland for the first time.

A new species of the murid *Zyzomys* from the Pliocene Rackhams Roost Deposit, northwest Queensland

GODTHELP, H. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

A new species of the murid *Zyzomys* is described on the basis of fossil material from Rackhams Roost, a Pliocene *Macroderma* roost site on Riversleigh Station. This species is dentally the most primitive of all known species of rockrats. It is the most abundant mammal species in the deposit. There is a similarly high abundance of *Zyzomys* species in more recent *Macroderma* deposits.

Temporal fenestration in a procolophonid reptile

HAMLEY, T. & THULBORN, T. 1994

Department of Zoology, University of Queensland, Queensland, 4072

The Late Permian and Triassic procolophonids were late survivors from the initial radiation of amniotes, and their skulls are usually thought to have retained the primitive anapsid condition, without temporal openings. However, two skulls attributed to *Procolophon trigoniceps*, from the Lower Triassic of South Africa, have been found to possess a lower temporal opening resembling that of the synapsid reptiles. The temporal opening was first discovered by H. G. Seeley 120 years ago, but its existence has been overlooked or denied in palaeontological literature for the past 90 years. Rediscovery of the temporal opening prompts us to examine the possible affinities of procolophonids and other 'parareptiles'. In doing so, we find no substantial support for the recent suggestion that procolophonids are the sister group of turtles.

Morphological changes in the Australian *Macroderma* lineage (Microchiroptera: Megadermatidae) from the Oligo-Miocene to the present

HAND, S. J. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

From the Riversleigh Tertiary deposits, eight megadermatids belonging to two lineages are now known. Morphological changes in the Australian *Macroderma* lineage are traced from the Oligo-Miocene to the present and comments are made on broader aspects of megadermatid evolution. In some Riversleigh deposits, there is evidence for sympatry of very differently-sized megadermatids. The Riversleigh megadermatids have provided an opportunity to trace an apparent trend to shorten the face in the *Macroderma* lineage from the Oligo-Miocene to the present and to examine a tendency to gigantism in independent megadermatid lineages.

A new and distinctive Oligo-Miocene hipposiderid (Microchiroptera: Hipposideridae) from Riversleigh Station, Queensland

HAND, S. J. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

A large, new and very distinctive hipposiderid is described from complete skull material recovered from the Oligo-Miocene Bitesantennary cave deposit located on the south-eastern margin of the D-Site Plateau, Riversleigh Station, north-western Queensland. The species is compared with Tertiary French and Australian species of *Brachhipposideros* as well as Quaternary Australian hipposiderids (genera *Rhinonictis* and *Hipposideros*). The phylogenetic relationships of the new bat and apparent problems in current hipposiderid taxonomy are discussed.

Scaly-foots and pointy teeth: pygopod mandibular variation and first fossil record from the Miocene of Queensland

HUTCHINSON, M. N. 1994

South Australian Museum, Adelaide, South Australia, 5000.

The snake-like pygopod lizards are a group of 35 species confined to Australia and New Guinea. They are gekkonoid, but their phylogenetic relationship to typical geckoes is not yet well established. Recent morphological and emerging biochemical data point to a sister group relationship with, or possibly within, the Australian diplodactyline geckoes. Pygopods show considerable variation in mandibular and dental structure, correlated with dietary specialisation in several genera. This variation is summarised and employed in identifying the first fossil member of the family to be reported, a partial dentary, from the early Miocene of the Riversleigh area, northwestern Queensland, Australia. The fossil is most similar to the living genus *Pygopus* but differs in its more evenly-sized teeth.

The Neogene radiation of Australian sharks: real or apparent ?

KEMP, N. R. 1994

Tasmanian Museum, Hobart, Tasmania, 7000.

By the Mid-Tertiary all eight orders of Neoselachians – modern sharks – were represented in Australia. Numerically, the Lamniformes (mackerel sharks) dominate the Tertiary record. The Palaeogene is well represented by the Odontaspidae and the Mitsukurinidae, by *Carcharias* (grey nurse sharks) and *Scapanorhynchus* (goblin sharks), respectively. The Odontaspidae continue through to the Recent with large numbers of teeth being preserved, especially in the Neogene. However, the Lamnidae dominate the Neogene in the number of species, with up to a dozen taxa representing at least four genera: *Carcharodon* (white pointers), *Carcharoides* (serrated porbeagles), *Isurus* (makos) and *Lamna* (porbeagle). The presence of at least seven species of *Isurus* in Australia in the Neogene may be indicative of a southern centre of radiation for this genus; nowhere else do all these species occur together. The Carcharhiniformes (ground sharks) which today contain, world-wide, more than half of all shark species are relatively poorly represented in Australian Neogene deposits, and are conspicuous by their virtual absence from the Palaeogene. Of this order, *Carcharhinus* (whalers) is the most common taxon, followed by *Galeocerdo* (tiger shark), *Galeorhinus* (school shark), *Hemipristis* (snaggleteeth shark), and *Sphyrna* (hammerhead sharks) which is known from only a few teeth. The Hexanchiformes (six- and sevengill sharks), Pristiophoriformes (saw sharks), Heterodontiformes (bull sharks) and Orectolobiformes (wobbegongs) are known variously throughout the Tertiary, but are certainly not common. The Squaliformes (dogfish sharks) have yet to be found. The influence of the warmer Miocene temperatures – which would be expected to result in an increase in the number and variety of sharks in southern Australian seas is not reflected in the local fossil record. The presence in the Australian Neogene of many species of *Isurus* is real, the numerical dominance of *I. hastalis* is due to a collecting bias, *Carcharias* is definitely a common taxon. The relative paucity of most other shark taxa may be due to depositional features such as fossiliferous winnowed deposits, and lack of preservation of certain environments of deposition.

Studies of the Late Cainozoic diprotodontid marsupials of Australia 1. Revision of the genus *Euowenia*

MACKNESS, B. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

Species of the genus *Euowenia* are rare taxa in Australian faunal assemblages. Two species have been described: *Euowenia grata* (De Vis 1887) on the basis of a partial cranium and dentary from Chinchilla, Queensland and *E. robusta* (De Vis 1891) from dentaries found at Freestone Creek, near Warwick, Queensland. Woods (1968) suggested that *E. robusta* was a junior synonym of *Nototherium inerme*. Mackness (1988) identified *E. robusta* as a zygomaturine and this taxonomic assessment is confirmed here. A number of additional specimens of *Euowenia* have been recovered from northern Australia including a new species, described here on the basis of a partial cranium and lower dentary featuring relatively unworn teeth. This additional material has highlighted a number of useful synapomorphies for *Euowenia* and a new generic diagnosis is provided. Additional published records of *Euowenia* are examined in the light of this new diagnosis. A significant extension in range and chronology is reported. A guide to identifying isolated *Euowenia* teeth from those of other northern Australian diprotodontids is also provided. The late Miocene *Meniscolophus mawsoni* is shown to share many synapomorphies with the genus *Euowenia* and a new taxonomic position is proposed for this taxon.

Studies of the Late Cainozoic diprotodontid marsupials of Australia 2. The identity of *Zygomaturus macleayi* Krefft and *Z. creedii* Krefft

MACKNESS, B. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

A partially reconstructed palate with left and right P³–M⁵ was described from the Condamine River, Queensland by Krefft in Longman (1921) as *Zygomaturus macleayi*. Longman recognised that the P³ of *Z. macleayi* was not the same as *Z. trilobus* but could not make any definitive taxonomic assignment. It is confirmed here that the holotype does not represent a zygomaturine based on its P³ morphology. Another right P³–M⁵, figured by Owen (1872) as *Nototherium inerme* and a cast of a left P³–M⁵ (BMNH M5002 labelled *Nototherium mitchelli* although presumably from the same animal) represent additional specimens referable to *Zygomaturus macleayi*. Woods (1968) suggested that the identification of the Owen illustration as *Nototherium inerme* was correct. This cannot be the case, however, as the molar row gradient of *Zygomaturus macleayi* is substantially different to all *Nototherium* holotypes and lectotypes, even allowing for allometric distortion. *Zygomaturus macleayi* cannot be placed in any existing diprotodontid genus although it does share many features in common with the Pliocene *Euryzygoma*. It is therefore placed in a new monotypic genus.

Zygomaturus creedii was described by Krefft (1873) on the basis of a fractured right premaxilla with I¹ and other incisor fragments. Only the incisor remains in the Australian Museum. The holotype is indistinguishable from other I¹'s from *Zygomaturus trilobus* and therefore *Z. creedii* is regarded as its junior synonym.

Studies of the Late Cainozoic diprotodontid marsupials of Australia 3. Key to the identification of lower molars

MACKNESS, B. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

The fossil remains of diprotodontids are commonly found as isolated molars or as dentary and/or

maxillary fragments. A lack of recognisable genera-specific features has resulted in confusing taxonomic assignments. Examination of an extensive collection of late Cainozoic dentary fragments from Australia has revealed a number of features useful for distinguishing genera. The poster presents a key to the identification of the lower molars of *Diprotodon*, *Euowenia*, *Euryzygoma*, *Nototherium* and *Zygomaturus*. This, along with a guide to the lower premolars presently in preparation by Mackness should provide the basis for more consistent determination of diprotodontid species diversity and distribution in the late Cainozoic of Australia.

An enigmatic family of marsupials from the Early Pliocene Bluff Downs Local Fauna of northeastern Queensland

MACKNESS, B., ARCHER, M. & MUIRHEAD, J. 1994

School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.

Discovery of a right mandible from the early Pliocene Bluff Downs Local Fauna of the Allingham Formation, northeastern Queensland, provides evidence for a highly specialised group of marsupials that has no previously known representatives. Key features are tribosphenid-like molars with elaborate buccal and anterior cingula, unique buccal cusps, complex cusp and crest relationships in a gradient that increases from M_5 to M_2 , complex P_3 morphology including an elaborate posterior cusp and a prominently bicuspid P_2 . The M_5 and M_4 have some features reminiscent of peramelemorphians but none of these are undoubted synapomorphies. The M_2 and premolars exhibit other features that are diprotodontian-like although these may be convergent. Some aspects of lower morphology most closely resemble those seen in late Cretaceous glasbiids from North America and early Tertiary didelphimorphs (possibly glasbiids) from South America. These resemblances too are most likely to be convergent. Precise occlusal and possibly thegotic wear on all blades indicates that this extraordinary morphology is matched by precise occlusal counterparts in the as yet unknown upper dentition rather than abnormal and that this individual lived for a long time. Because there are no undoubted synapomorphies shared with any previously known family, we propose a new monotypic family for this taxon. Its highly distinctive morphology suggests antiquity that well predates the early Pliocene and demonstrates that not all contemporary lineages of middle Tertiary marsupials were sampled by the otherwise diverse Oligo-Miocene communities of South Australia and Queensland.

The Spring Park Local Fauna, a new Late Tertiary fossil assemblage from northern Australia

MACKNESS¹, B., MCNAMARA², G., MICHNA³, P., COLEMAN³, S. & GODTHELP¹, H. 1994

1. School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.
2. Department of Geology, James Cook University, Townsville, Queensland, 4811.
3. Townsville Grammar School, Townsville, Queensland, 4811.

Preliminary investigation of a series of complex freshwater, fluvial quartz sand and clay deposits from Blaggard Creek, northwest of Charters Towers, northeastern Queensland has revealed a rich collection of fossils. The fauna, here named the Spring Park Local Fauna, contains: *Zygomaturus* sp. cf. *Z. trilobus*, a new species of *Euowenia*, *Palorchestes parvus*, another palorchestid, a phascolarctid, several macropodids, *Pallimnarchus* sp. cf. *P. pollens*, a new crocodilian and a python as well as remains of turtles and fish. The deposit is subjacent to Pliocene basalts. Sediment grain size and sedimentary structures mitigate against the idea that the deposit may have resulted from accumulation at the edge of a basalt bluff and suggests a stream too large to have been in this position after basalt deposition. Therefore, the deposit is nominally assessed as being of Pliocene age based on its geomorphology and biocorrelation with Chinchilla and Bluff Downs faunas.

Three-dimensional analysis of variation in marsupial teeth using computed tomographic scans

MACKNESS¹, B. & SELDON², L. 1994

1. School of Biological Sciences, University of New South Wales, Kensington, New South Wales, 2033.
2. Department of Otolaryngology, University of Melbourne, Parkville, Victoria, 3052.

The analysis of variation in the diagnostic P³ of *Zygomaturus trilobus* has been undertaken by means of computed tomography. The study was carried out in conjunction with the Cochlear Implant Program of the Department of Otolaryngology, University of Melbourne, which uses computed tomographic scans for reconstructing intricate anatomical features such as the temporal bone to assist surgeons. The input data was obtained via a series of CT scans taken at 1.00 mm intervals, from the alveolus to the tooth crown, on a suite of isolated P³ teeth suspended in a polystyrene foam collar. The scans, on film, were then digitised from a light box using a Panasonic WV-BL200 video camera connected to a IBM AT compatible personal computer and stored in a CompuServe GIF graphics interchange format. A Data Translation DT2851 medium resolution video card with 512 x 512 pixels and 256 colours was the only 'special' piece of hardware used in the study. An automatic edge detection system was used to combine the scanned images to form a 3D computer model. Automatic analysis of a number of variables was then possible. This included plotting the ratio of the length and width along the entire midline of the tooth at 1.00 mm intervals. Individual teeth were also divided into four quadrants and analysed for shape using the formula $(10-40\pi A / P^2)$ as well as for volume and surface area. The study highlights the effectiveness of computers in assessing previously subjective characters such as 'shape', surface area and quadrant volumes as well as providing a suitable technique for close examination of variation in a number of isolated individuals.

The morphology and relationships of thelodonts, Siluro-Devonian agnathans

MARSS¹, T. & RITCHIE², A. 1994

1. Institute of Geology, Tallinn, Estonia
2. Australian Museum, Sydney, New South Wales, 2000.

Thelodonts are a group of poorly-known Siluro-Devonian agnathans characterised by a micromeric dermal skeleton consisting entirely of small scales. Complete thelodonts are very rare but articulated specimens are known from sites in Scotland, England, Estonia, Norway and Canada. Isolated scales, by contrast, are often locally abundant, widely distributed in Siluro-Devonian sediments and are being increasingly used in biostratigraphic studies world-wide, including Australia and Antarctica. Recent discoveries of articulated thelodonts provide new information on the variation in shape of thelodont scales in different parts of the dermal skeleton, the position of the eyes, the nature of the mouth and the branchial apparatus, the size and the shape of the lateral, dorsal, ventral and caudal fins. The relationships of thelodonts with other Palaeozoic agnathans will be discussed.

The Late Miocene Ongeva Local Fauna from the Waite Formation of central Australia

MEGIRIAN¹, D., MURRAY¹, P. F. & WELLS², R. T. 1994

1. Northern Territory Museum, Darwin, Northern Territory, 0800.

2. Flinders University of South Australia, Bedford Park, South Australia, 5042.

The Ongeva Local Fauna (LF) from the Waite Formation of central Australia is biochronologically significant because it is in lithostratigraphic superposition to, and unconformably separated from, the Alcoota LF. It contains a zygomaticurine diprotodontid (description in press) that is structurally intermediate between *Kolopsis torus* Woodburne from the Alcoota Local Fauna, and *Zygomaturus gilli* Stirton from the Beaumaris LF of Victoria. *Kolopsis torus* is also present in the Ongeva LF, though the Ongeva LF specimens differ slightly in some measurements from the Alcoota population. A morphospecies distinction of the two populations is not justified on the available evidence. The indications are that a cladogenetic event occurred in the Zygomaticurinae between Alcoota and Ongeva LF times, an interpretation consistent with the presence of a *Zygomaturus* sp. and a *Kolopsis* sp. in the younger Beaumaris LF. Dromornithidae are also common elements in the Ongeva LF, but have not yet been analysed in detail. The indications are that a *Dromornis* sp. cf. *D. stirtoni* and an *Ilbandornis* sp. are present. A crocodilian, *Quinkana* sp., is represented by a dentary and a relatively large number of ziphodont teeth. The most remarkable fossils, however, are large, loosely-deposited coprolites draped over the bones. Two quarries are now producing Ongeva LF material, but their yields may eventually be limited by the huge overburdens that accompany excavating into the sides of steep hills.

Late Cainozoic crocodilians collected by the 1980 and 1983 FUAM Expeditions into the Lake Eyre Basin of South Australia

MEGIRIAN¹, D., WELLS², R. T. & TEDFORD³, R. H. 1994

1. Northern Territory Museum, Darwin, Northern Territory, 0800.

2. Flinders University of South Australia, Bedford Park, South Australia, 5042.

3. Department of Vertebrate Paleontology, American Museum of Natural History, New York, N. Y., 10024, United States of America.

The Flinders University-American Museum of Natural History (FUAM) collection of crocodilian material from Pliocene and Pleistocene strata of the Lake Eyre Basin is just one of several collections made since 1892. Virtually none of the material of this geological age and provenance has been described, but has been variously assigned to the extinct form *Pallimnarchus pollens* de Vis, or to the extant species *Crocodylus porosus* Schneider. The distinction of fragmentary remains of these two taxa has proved difficult in the past. Poor stratigraphic control has also hampered the interpretation of crocodilian succession. The stratigraphy of the Lake Eyre Basin Pliocene and Pleistocene has now been resolved in some detail, and the stratigraphic provenance of the FUAM material is recorded. There is *prima facie* evidence in the FUAM collection, from specimens that could not have been re-worked, for the presence of a *Pallimnarchus*-like form in the mid Pliocene (estimated age: 3.9–3.4 Ma) Tirari Formation and the late Pleistocene (estimated age, 0.2 Ma) Kutjitara Formation. There is no evidence in the FUAM collection for the presence of a *Crocodylus*-like form in the Tirari Formation. One *Crocodylus*-like specimen from the Kutjitara Formation differs in preservation from other material of that provenance and is possibly reworked. Only two potentially diagnostic specimens were collected from the latest Pleistocene (estimated age: 0.04 Ma) Katipiri Formation: a jugal that may be referable to *Crocodylus*, and a maxillary fragment most closely resembling *Australosuchus clarkei* Willis and Molnar from the mid-Tertiary Etadunna Formation which forms the basement to the Pliocene and Pleistocene strata.

Post-cranial descriptions of *Ilaria* and *Ngapakaldia* (Vombatiformes, Marsupiala) and the phylogeny of the vombatiforms based on post-cranial morphology

MUNSON, C. 1994

Moreno Valley, CA 92553, United States of America.

The post-crania of the vombatiform marsupial *Ilaria illumidens* from medial Miocene strata of South Australia are described and compared to those of other vombatiforms, with the observation that *Ilaria* shares a similar morphology of the manus and pes with living wombats. While this indicates a certain degree of fossorial activity, the size and vertebral morphology of *Ilaria* argue against a burrowing lifestyle. Another medial Miocene vombatiform, *Ngapakaldia tedfordi*, is described as having a plesiomorphic vombatiform skeleton similar in many ways to that of the phalangeriform possums, but with adaptations for greater size and a plantigrade, terrestrial habitus. Besides stouter and more robust limbs, these adaptations are evident in the concave dorsal surface and laterally facing fibular facet of the astragalus that creates a less flexible upper ankle joint.

For this study, a cladistic analysis was made using the post-crania of all the families in the Vombatiformes and several species representing outgroups, in order to establish synapomorphies uniting the group and to evaluate the position of these two genera within it. The results indicate that the ilariids and vombatids probably share a common ancestor, based on the similarity of the metapodials and phalanges, especially the uniquely identical morphology of the proximal metapodial facets. *Ngapakaldia*'s similarity in form to phalangeriform possums reflects the arboreal ancestry of the vombatiform clade and indicates the plesiomorphic state from which the post-crania of other, more specialised vombatiform families (i.e. fossorial wombats and ilariids) are derived.

Recent *Diprotodon* discoveries in South Australia

PLEDGE, N. S. 1994

South Australian Museum, Adelaide, South Australia, 5000.

From the early days of the colony, *Diprotodon* remains have been found. Prior to the Lake Callabonna discoveries, the best were a skull from near Gawler in 1891 (now apparently lost) and a skull from Baldina Creek near Burra in 1890. Since 1970, and the publicity engendered by the expedition to Lake Callabonna in that year, four chance discoveries have been made in the Adelaide area, and two on the West Coast. More material has been obtained from a Port Pirie site, and minor records made for the Woomera area, Morgan and Naracoorte.

A badly tumbled and rolled molar found in beach gravels at Hallett Cove in 1970 may now be related to a partial pelvis and other bones and teeth found in 1992 in the banks of the Field River which flows into the southern end of the cove. Soil samples from this site have been taken for thermoluminescent dating by Prof. J. Prescott, University of Adelaide. A similar discovery was made in early 1993 in the Little Para River, near Salisbury. In 1980, a jaw fragment was found in a sewer trench near Darley Road, Paradise, on the River Torrens. *Diprotodon* jaws and other bones have been found in lithified Bridgewater Formation (coastal dune sand) at Sheringa Beach, west of Port Lincoln, and also near Head of the Bight, west of Ceduna. These bones are well preserved but firmly embedded in the rock. Jaws and a partial skeleton have been recovered from an old locality – a sand quarry near Port Pirie, but have been damaged by the bulldozers. A poorly preserved skeleton is known in Elizabeth Creek which flows into Pernatty Lagoon near Woomera.

Mineralised tooth fragments have been collected from river alluvium excavated from a farm dam near Morgan, on the River Murray, and several teeth were found during excavations in Henschke Fossil Cave at Naracoorte. Bones embedded in reef rock at a depth of five metres off Victor Harbor have been reported but not yet confirmed.

A new extinct sthenurine kangaroo (Marsupialia, Macropodidae) from southeastern Australia

PRIDEAUX, G. J. & WELLS, R. T. 1994

School of Biological Sciences, Flinders University of South Australia, Bedford Park, South Australia, 5042.

A new species of *Simosthenurus* is described from Late Pleistocene deposits in southeastern South Australia, western Victoria, northern and southeastern New South Wales, northwestern Tasmania and the Nullarbor Plain, Western Australia. The species is similar in size and mandibular morphology to *Simo. browni*, but its cranium is more dolichocephalic with a less inflated nasal region. The dentition is distinctive and, although similar in size to *Simo. occidentalis*, several molar characters appear closer to *Sthenurus andersoni* in morphology. Because the new species exhibits features previously only considered typical of either *Simosthenurus* or *Sthenurus*, a thorough reassessment of sthenurine generic relations is impelled. Whether or not the distribution of craniodental character states within the groups confirms the tentative placement of this new form within *Simosthenurus*, it probably evolved soon after split of the *Simosthenurus* and *Sthenurus* lineages.

An ornithomimosaur and protoceratopsian from the early Cretaceous of southeastern AustraliaRICH¹, T. H. & VICKERS-RICH², P. 1994

1. Department of Paleontology, Museum of Victoria, Melbourne, Victoria, 3000.

2. Department of Earth Sciences, Monash University, Clayton, Victoria, 3168.

Ornithomimosaurs were intermediate-sized, agile, edentulous theropod dinosaurs best known from the late Cretaceous of the Northern Hemisphere. Fragmentary records of them exist there in the early Cretaceous and possibly the late Jurassic. *Elaphrosaurus bambergi* from the late Jurassic Tendaguru of Tanzania is likely to be a primitive member of this group of dinosaurs.

A pair of femora, one of an adult and one of a juvenile about 45% as large as the former were found at the late Aptian – early Albian Dinosaur Cove site, Victoria, Australia, in 1991. The relatively large size of the lateral distal condyle in comparison to the medial distal condyle characterises these specimens and the ornithomimosaurs among theropods (Barsbold & Osmolska 1990). The lesser trochanter is plesiomorphic-primitive in being less expanded than is typical of the well known late Cretaceous ornithomimosaurs.

Ceratopsians are common late Cretaceous dinosaurs of North America and Asia with questionable records from Europe and South America. None have previously been reported from the early Cretaceous. An ulna recovered from early Aptian sediments of the Strzelecki Group at the Arch near Kilcunda, Victoria, Australia, shares the foreshortened and mediolaterally compressed form characteristic of ceratopsians and not known in other vertebrate groups. In particular, the Australian specimen is remarkably similar in both size and morphology to an ulna of *Leptoceratops gracilis* from the Maastrichtian of Alberta, Canada.

The presence in the early Cretaceous of Australia of two dinosaur groups best known from the late Cretaceous of the Northern Hemisphere suggests that an hypothesis of either's origin on the Gondwana continents should not be rejected out of hand.

BARSBOLD, R. & OSMOLSKA, H., 1990. Ornithomimosauria. Pp. 225–248 in 'The Dinosauria' Ed. D. B. Weishampel, P. Dodson & H. Osmolska. University of California Press: Berkeley.

The molar / premolar boundary in the macropodiforms: cracking the code of molar cusp patterns in the transitional zone

RIDE, W. D. L. 1994

Department of Geology, Australian National University, Canberra, Australian Capital Territory, 2600.

The striking functional discontinuity at the molar/premolar boundary of many macropodiforms (kangaroos, wallabies and rat-kangaroos) is reflected in cusp pattern modification in the deciduous premolar and the first molar. Following recent analysis of this in *Jackmahoneya*, other propleoplinines, and *Hypsiprymnodon*, the analysis is extended to the Macropodidae.

The great Canowindra Devonian fish kill

RITCHIE, A. 1994

Australian Museum, Sydney, New South Wales, 2000.

The richest fossil fish site in Australia, evidence of a unique Late Devonian mass fish-kill, was first discovered in 1956 near Canowindra, N. S. W. Using a 22 tonne excavator, Alex Ritchie relocated the fish horizon in January 1993. Preliminary excavations indicate that the site contains hundreds, probably thousands, of complete fish specimens. Five taxa have been recognised to date. Three types of armoured fishes, placoderms, are present. Antiarchs (*Bothriolepis* and *Remigolepis*) are dominant, forming about 95% of the fauna. An arthrodire (*Groenlandaspis*) is present but is extremely rare. The fourth type present is a crossopterygian, an elongate, air-breathing, lobe-finned fish named *Canowindra* after the town near where it was discovered. The January '93 excavation turned up four new crossopterygian specimens of a new form, different from *Canowindra*. Two of these were giants, over 1.5 m long.

Alex Ritchie hopes to carry out a major excavation at Canowindra in June, using logistic support provided by the local shire council and enlisting local high school students as volunteers. The enormous scale and importance of this fossil site is now clear – there could be several hundred tonnes of rich fish-bearing slabs awaiting recovery, easily excavated and readily accessible in a roadside locality! The great Canowindra Devonian fish-kill provides a unique opportunity for a detailed population study on an entire fauna, killed suddenly and buried quickly. Given sufficient community support and funding Canowindra has enormous potential for a major tourist, educational and scientific attraction for central west New South Wales.

Burnt ratite eggshell from Pleistocene aeolian sediments

SMITH¹, M. A., MILLER², G. & VAN TETS^{1,3}, G. F. 1994

1. Department of Prehistory, Australian National University, Canberra, Australian Capital Territory, 2600.

2. Center for Geochronological Research, University of Colorado, Boulder, CO, 80309, United States of America.

3. CSIRO Division of Wildlife & Ecology, Lyneham, Australian Capital Territory, 2602.

The history of *Genyornis newtoni* (Dromornithidae: Aves) is complicated by uncertainty surrounding the date of extinction and role of human predation. Work in progress near Wood Point, on the eastern side of Spencer Gulf, S. A., has revealed a thin horizon of burnt *Genyornis* and *Dromaius* eggshell stratified within a Pleistocene dune core. Dates of 47 ± 5 ka have been obtained for the eggshell of both ratite species using the protein diagenesis (amino acid racemisation) method. These dates are amongst the most recent obtained for *Genyornis* in a large series of such determinations on eggshell across the southeastern sector of the arid and semi-arid zone and suggest that this species was extinct over a large part of its former range by ca. 40–50 ka. Work is in progress to verify the AAS results using other dating methods, including AMS C14 on the eggshell and TL on the dune sediments. Several features of the site suggest a human agency for the accumulation of the eggshell.

Lake Callabonna: 'Veritable necropolis of gigantic extinct marsupials and birds'

TEDFORD, R. H. 1994

Department of Vertebrate Paleontology, American Museum of Natural History, New York, N.Y., 10024, United States of America.

The famous fossiliferous deposit at Lake Callabonna, northern South Australia, lies at the base of the local Quaternary sequence in laminated clays and fine sands tentatively correlated with the Millyera Formation of nearby Lake Frome. At Lake Callabonna these deposits accumulated in a lake of variable salinity, several times the size of the present saltpan. Plant remains contained in the deposits indicate a

more arborescent flora than occurs near the lake today but one containing taxa still living in the region. This and stratigraphic evidence suggests a seasonal, yet wetter than present, climate with a fluctuating water-table. Geological correlations with Lake Frome suggest a medial Pleistocene age, 0.1–0.7 Ma, as the span during which the Callabonna fauna lived.

The large-bodied vertebrates were mired while walking across the lake floor when the surface appeared dry but the underlying clays were water saturated. This mode of accumulation has yielded articulated skeletons of taxa known elsewhere only from fragments. In addition to the well-known remains of *Diprotodon optatum* and possibly a second, smaller species, there are three species of *Sthenurus*: a new giant form, the somewhat smaller *S. tindalei*, and the considerably smaller *S. andersoni*. Other kangaroos include: *Macropus* sp. cf. *M. titan*, a smaller *Macropus* sp., and *Protemnodon* sp. cf. *P. brehus*. Skeletons of *Phascolonus gigas*, the dromornithid *Genyornis newtoni*, and an emu similar to the living species are also present.

The Lancefield megafauna site, Victoria

VAN HUET, S. 1994

Department of Earth Science, Monash University, Clayton, Victoria, 3168

The Lancefield Quaternary megafaunal site was the third megafaunal locality to be discovered in Australia. There are three separate sites located at Lancefield; the Classic, located in 1974, the South, located in 1983 and Maynes Site, first discovered in 1843 and subsequently relocated in 1990. The cause of the death of the megafauna at Lancefield is related to climatic changes occurring across Australia at the time of the collection. These changes had a detrimental effect on the habitats of browsing megafauna and their ecologically dependent carnivores and scavengers. Disease may have affected animals that were in a weakened state through lack of food and water.

The presence of large numbers of bones in a concentrated area is due to transportational processes. The topographical nature of the area and the characteristic Quaternary climate encouraged major seasonal rainfall and sheet flooding. Bias in the collection is also due to transportational processes. Abrasion during transportation led to the destruction of the more fragile elements and weathering would have added to the bones fragility and subsequent fragmentation. Other biases in the collection, such as up to 90% of the elements being identified as the species *Macropus titan*, and the absence of juveniles of this species may well be related to the climatic conditions and subsequent habitat changes in the area at the time.

Functional anatomy of the Lake Callabonna sthenurine kangaroos

WELLS¹, R. T. & TEDFORD², R. H. 1994

1. School of Biological Sciences, Flinders University of South Australia, Bedford Park, South Australia, 5042.
2. Department of Vertebrate Paleontology, American Museum of Natural History, New York, N.Y., 10024, United States of America.

This paper reports on our functional anatomical study of three species of the extinct kangaroo *Sthenurus* from Lake Callabonna, northern South Australia. Complete skeletons of these animals were recovered from the lake sediments thereby providing an unparalleled opportunity for comparative anatomical study. The large taxa show sexual dimorphism. All differ from extant *Macropus* species in having short deep skull, long forefeet with reduced lateral digits, and functionally monodactyl hindfeet. The hand is modified for grasping, the forelimb may be raised above the head to reach high browse; the vertebral column shows limited flexion, but considerable extension in the anterior end; the pelvis is modified for flexion and adduction of the thigh; the hindlimb is more massive than *Macropus* species, and although of similar proportions there is greater emphasis on tendons and ligaments to augment muscular action. The mechanics of movement in these extinct species will be discussed.

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